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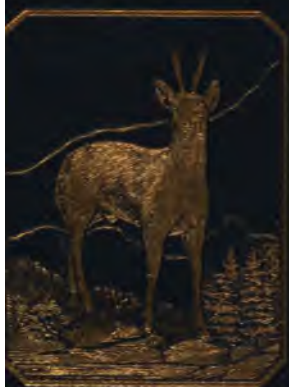
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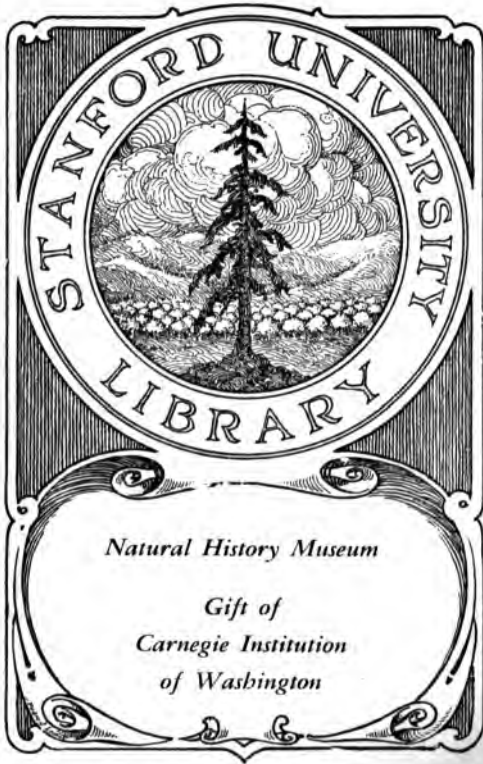
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ANIMALS



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EUROPEAN ANIMALS



IRISH SCENERY WITH THE IRISH HARE (*Lepus timidus*) AND GROUSE (*Lagopus scoticus*) IN THE FOREGROUND. PHOTOGRAPHED FROM A LIFE GROUP IN THE DUBLIN MUSEUM.

EUROPEAN ANIMALS:

THEIR GEOLOGICAL HISTORY AND
GEOGRAPHICAL DISTRIBUTION

BY

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PREFACE.

THE method of treatment of the subject discussed in this work was adopted by me when delivering the Swiney Lectures on Geology last year, at the Victoria and Albert Museum in London.

Dr. Wallace's remark that we may be enabled, by an accurate knowledge of any group of birds or insects and of their geographical distribution, to map out the islands and continents of a former epoch, encouraged me to attempt to apply his ideas in dealing with our own Continent, and to extend them to other groups of animals.

Professor E. Forbes was the first to recognise the significance of the geographical distribution of living animals in deciphering their past wanderings, and I have approached the investigation of the geological history of our fauna in the manner indicated by him. I thought that this method would convey to the general reader, as well as to the student, a clear conception of the nature of the problems to be solved.

I trust that this work will stimulate the researches of the student of systematic Biology and that it may also prove acceptable as a contribution to the past geographical history of our Continent.

Professor Ray Lankester, the Director of the British Museum (Natural History), urged me to publish my lectures, and promised me every facility in suitably illustrating this work by photographs taken from specimens in his charge. I have

availed myself of this kindness in many instances. My gratitude is also due to Messrs. Th. G. Fisher, to Messrs. Macmillan, to H.M. Stationery Office, and to Mr. Madison Grant for allowing me to copy illustrations from works issued by them.

To the many friends who have given me information or assistance I beg to tender my sincere thanks. Especially am I indebted to Sir Henry Howorth, who not only read through my rough proofs, but was good enough to make numerous corrections and critical notes, which were most valuable to me. Dr. F. Oswald, the author of the recently published work on the Geology of Armenia, suggested some additions, while Mr. W. E. Sharp, Mr. W. Evans, Mr. A. S. Kennard, Mr. Robert Welch, Mr. R. Le Praeger, Mr. T. W. Lyster and Mr. J. X. King gave me valuable assistance or information.

In laying this work before my readers, I am conscious of its many defects, arising to some extent from the wide range of the subject. It leaves many points inadequately treated. But I venture to hope that naturalists will assist me in rendering my future researches more complete by sending me notes of any important omissions or corrections.

R. F. S.

TUDOR HOUSE,
DUNDRUM, CO. DUBLIN,
January 17th, 1907.

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EUROPEAN ANIMALS.

CHAPTER I.

THE geological history of our animals is largely the history of their past wanderings. And just as in geology the study of the present supplies us with a key that opens the secrets of the past, so a search for the nature of the bygone wanderings of our animals is revealed to us by their actual geographical distribution. By carefully observing how the dispersals of animals are brought about nowadays, we are enabled to judge of the dispersals of the past.

A great many noteworthy facts have been collected together by Lyell, Darwin¹ and others, to demonstrate the facilities possessed by species for accidental or occasional means of dispersal. For, though Darwin admitted that great mutations of land and sea had occurred within the period of existing organisms, he paid a good deal of attention to experiments illustrating the possibility of lighter objects, such as seeds, insects or shells, being carried by marine currents across the sea from the mainland to an island.

With the view to testing his theory, Darwin immersed a number of specimens of the Roman snail (*Helix pomatia*) (Fig. 24) in sea water, and found some of them to withstand an immersion for twenty days. During this length of time, he remarks, the shell might have been carried, by a marine current of average swiftness, to a distance of 660 geographical miles.

After all these experiments, Darwin acknowledged that it did not seem to him likely that land shells had often been transported in that way across the sea to an island. He suggested

¹ A list of the books and papers consulted in preparing this volume will be found in the Appendix.

that possibly young snails might sometimes adhere to the feet of birds, and thus be carried to long distances from their home.

Baron Aucapitaine has since tried similar experiments, which have been even more successful. He immersed a dozen specimens of another mollusc (*Cyclostoma elegans*) in sea water for a fortnight, and out of these eleven survived. This snail possesses a lid or operculum, with which it can close the mouth of its shell, and this fact no doubt contributed to the remarkable success of Aucapitaine's experiment.

We may take it for granted that owing to its possession of an operculum this snail is endowed with exceptional facilities for being carried from the western parts of Europe, where it is common, to distant islands. And yet it does not inhabit the Canary Islands, Madeira, or even Ireland, none of which are at too great a distance to be within easy reach for a floating object. The fact that this shell does not occur living in Ireland is of particular interest, because dead shells have frequently been picked up on its shores, indicating that marine currents actually do carry specimens, and have probably transported living ones to that island for many centuries. That *Cyclostoma elegans* has nevertheless failed to establish itself in Ireland seems to justify the belief that other snails less adapted for ocean transport, or slugs, would have no chance of doing so.

As for Darwin's theory that birds might occasionally carry young snails on their feet across the sea, this subject has been very carefully investigated since his time. It has been shown by Mr. Winge and Dr. Andersen, who have examined the legs and wings of many thousands of migratory birds just after crossing the sea, that their legs were clean; and no seeds or other objects were found adhering to their feathers, beaks or feet. It has also been proved that birds migrate on empty stomachs.¹

After years of patient research on the origin of the fauna of Celebes, Dr. Sarasin came to the same conclusion: that birds are of little importance in influencing the dispersal of other animals.

¹ Dr. Knud Andersen of Copenhagen informed me of these facts by letter.

Although the occasional or accidental transport of species by wind or by marine currents has probably taken place sometimes, it does not as a rule seem to affect the constitution of an island fauna very materially. The influence of man, however, on a fauna is an important factor.

Mr. Kew, who has occupied himself specially with the subject of accidental distribution, and whose little book on the subject is well known, is of opinion that, as far as mollusca are concerned, human agency has influenced their dispersal more than all other causes taken together. Man is probably the most powerful of all agents in the occasional transmission of species across natural barriers, and his actions may be accidental as well as intentional. Hence among animals possibly introduced by man we have to distinguish between those disseminated all over the world by pure chance and such as have been carried into new countries purposely. Snails, centipedes, woodlice, beetles and cockroaches are constantly being unintentionally carried with vegetables, fruits and shrubs from one country to another. Earthworms are sometimes transported in the balls of earth in which the roots of trees are enveloped.

Very frequently the animals which have been thus introduced from one country to another fail to permanently establish themselves. They sometimes linger on for a few years and then die out again. Occasionally, however, they reach suitable surroundings, and spread rapidly. As an example, I might mention our large garden snail, *Helix aspersa*, which is used as food by French and Portuguese sailors, and which has been exported to many foreign countries where flourishing colonies now exist.

As a rule, such intruders to the native fauna are readily recognisable, for they scarcely ever extend their range very far from human habitations. They are known now from almost every country in the world. But we must carefully guard ourselves against the conception that all cosmopolitan forms of animal life must necessarily belong to that class of human importations.

The mere fact of an animal possessing a wide range proves

its adaptability to varied climates, and frequently betrays its ancient origin.

It is quite possible, therefore, that many of our widely-distributed forms may owe their cosmopolitan range to the fact of their being very ancient. The genus *Pupa*, a small turret-shaped snail with a world-wide range, was already represented in the carboniferous deposits of North America. Another land-shell, called *Conulus*, from the same formation, likewise enjoys an extensive range. Some fresh-water species can be traced back to the Cretaceous period. In the countless ages which have passed since then, it is no wonder that certain animals should have acquired a world-wide range.

We may regard it, therefore, as an established fact that accidental dispersal of a species is the exception, while slow progress on land for terrestrial animals is the rule.

As far as possible, I shall refer to well-known animals, in these studies of the European fauna, for it is obvious that I can only mention a mere fraction of the immense number of species to be found on our Continent. Sometimes, however, I shall allude to such animals which appear to me of particular importance from a distributional point of view, though they may be inconspicuous and more or less unknown to the great majority of my readers.

Every species of animal has its own area of geographical distribution, to which it is, as a rule, permanently confined. It will naturally tend to increase the boundaries of its range in every direction, unless prevented from doing so by some barrier which may be either a mountain range, a desert or the sea. The latter is the most formidable barrier.

When we find such a close relationship in the faunas of two countries as between those of England and France, or Greece and Asia Minor, we may be sure that the sea barrier which now exists was absent when the animals crossed from the one area to the other. Similarly when we notice a very striking difference in the fauna of two parts of a country, such as between southern and northern Spain, which cannot be explained from its present configuration, we may assume that

a powerful barrier formerly existed which separated these two areas. We can thus ascertain the gradual changes which have occurred in the distribution of land and water in Europe. From a careful study of the general range of groups of species, we can gather also the direction of their advance. We have been able to trace, in this manner, that large assemblages of animals issued from various parts of Europe, invading new territories like conquering armies, and sometimes after their retreat leaving a few stray members behind as a standing testimony of their former invasions.

Island faunas are particularly useful in aiding us to estimate the comparative ages of such waves of invasion, for they frequently preserve the traces of the latter much longer than the continents, where, owing to keener competition, faunas are subject to more rapid modification.

We need not use for our purpose species of animals which might owe their dispersal to such accidental means as I alluded to.

For instance, in the nest of the small yellow ant, which lives in this country, as a rule, under stones or clods of earth, we frequently meet with a minute white woodlouse (*Platyarthrus Hoffmansseggii*) (Fig. 1). It lives in company with the ants and is unmolested by them. The latter apparently do not provide for it in any way, though it is quite blind. Now the same species of woodlouse occurs again in the burrows of the yellow ant in France. Here is a case, then, of a small and inconspicuous object, which yet could not possibly have passed from the one country to the other except by means of some former continuity of land.

I have now endeavoured to give some of the reasons for my belief in the profound importance of the present geographical distribution of animals as an indicator of their geological history. But we possess still other means to aid us in unravelling the history of our European fauna.

Though it is evident that, in the vast majority of cases, land and fresh-water animals leave no perceptible trace of their former presence, yet much has been preserved to us, and these



FIG. 1.—*PLATYARTHURUS HOFFMANSEGGII*, WITH ITS GEOGRAPHICAL DISTRIBUTION IN EUROPE MARKED IN BLACK.

remains are, of course, of immense value in our researches. It is especially the river and lake deposits which have yielded the remains of animal life. But the numerous caverns in limestone districts which have either offered shelter to various kinds of wild animals or which have been used by wolves, wild cats or hyænas as convenient store-houses for their prey, have preserved for us some valuable chapters of history.

These evidences of past distribution aid us materially in tracing the wanderings of our animals from one part of Europe to another, or even from beyond the boundaries of our Continent.

This leads us, then, to the consideration of the comparative importance of the various classes of animals as aids to historical zoogeography.

Mr. Lydekker is one of the chief supporters of the doctrine that mammals afford us the safest and truest indications of the latest changes which have taken place in the distribution of land and water, and no one can help appreciating the force of his arguments in their favour, after reading his very instructive work on the geographical history of mammals. Their present and past range in Europe, moreover, is now fairly well known, though many details still require to be worked out.

In some respects the snails are even of greater value, for the shells, left behind them after death, are readily preserved and identified; and many of the species, as I have pointed out, are of very great antiquity. Snails are bound to the soil almost unlike any other creatures, while their organs of locomotion are of a primitive nature. They are mostly indifferent to the nature and quality of the food supply or the conditions of climate, and can exist and spread under more adverse conditions than mammals. They are easily collected and studied, with the result that our knowledge of the geographical distribution of European snails and slugs is probably more complete than that of any other class of animals.

Nevertheless, other naturalists claim for their favourite groups that they deserve some recognition in ranking as important guides in geographical studies of the past.

Mr. Beddard has a good word to say on behalf of the

earth-worms, while Mr. Pocock makes an appeal for scorpions. Dr. von Ihering vindicates a claim for ants, Mr. Andrew Murray for beetles, and Dr. Ortmann for fresh water crayfish.

As a matter of fact, in all classes of the animal kingdom there are certain families or genera which, on account of their peculiar habits or mode of life, are eminently suitable as indicators of former changes in land and water.

Though we naturally connect Wallace with the foundation of the science of modern zoogeography, as the geographical distribution of animals is sometimes styled, Edward Forbes and Sir Charles Lyell forestalled him in many respects. Thus the doctrine of specific centres of distribution of plants and animals was put by Forbes to a practical test long before Wallace had made this branch of natural history his special study. It is particularly in connection with the geographical distribution of the animals of our own country that Edward Forbes became so deservedly famous.

Dr. A. R. Wallace gained his reputation in the East in the Malay Archipelago, and on his return he published not only his delightful and instructive travels, but his great works on "The Geographical Distribution of Animals" and on "Island Life." What his views were upon the subject I am discussing may be gathered from the following remark which he made in one of his earlier works: "It is certainly a wonderful and unexpected fact," he says, "that an accurate knowledge of the distribution of birds and insects should enable us to map out lands and continents which disappeared beneath the ocean long before the earliest traditions of the human race. Wherever the geologist can explore the earth's surface, he can read much of its past history, and can determine approximately its latest movements above and below the sea level; but wherever oceans and seas now extend he can do nothing but speculate on the very limited data afforded by the depths of the waters. Here the naturalist steps in and enables him to fill up this great gap in the past history of the earth."¹

It is not only animals of all kinds which are of use in solving

¹ Malay Archipelago, p. 14.

problems such as these raised by Dr. Wallace. As a rule, animals advance step by step, and thus steadily occupy new territories in their onward march across solid ground; botanists have urged that plants generally spread in precisely a similar manner.

Botany certainly took the lead in the science of geographical distribution. I need only mention the names of Humboldt, de Candolle, Heer, and Hooker. The latter's admission, that no material advance was made towards improving the laws of geographical distribution so long as it was believed that the continents and oceans had experienced no great changes of surface or of climate since the introduction of the existing assemblages of animals and plants, implies that he thoroughly believed in the importance of plants in the questions which here concern us. The great majority of botanists are impressed with the fact that plants wander just as animals do, not by saltatory movements, but by slow progression on land. We find therefore in great modern works such as Professor Engler's "History of Plant Development in the Northern Hemisphere," that the geographical distribution of plants is pressed into service to decipher the former mutations of land and water on our Continent, on the lines that I propose to adopt in this work.

Plants are in some respects more valuable than animals for our inquiries, for they are as a rule more affected by climate. The first place, indeed, has generally been assigned to plants as tests of former changes in climate, and our fossil forms have sometimes even been spoken of as thermometers of the past. It is especially in connection with the Glacial period¹ and its climate that certain plant remains occurring in glacial deposits have been adduced as evidence of an arctic temperature. When we remember, however, that alpine and arctic plants which are supposed to require a cold temperature can be well grown in a greenhouse atmosphere, we must recognise that implicit faith cannot be placed even in them.

I would also draw attention to the fact that on our own

¹ In employing the term "Glacial" in this connection, I do not intend to convey that I adhere to the general opinion as to the severity of climate prevalent during the geological period referred to.

shores plants of a sub-tropical nature can be grown in the open air almost side by side with arctic plants.

The mountain avens (*Dryas octopetala*) (Fig. 2) grows wild from



FIG. 2.—THE MOUNTAIN AVENS (*Dryas octopetala*).

sea level, in Ireland, up to considerable heights. Though abundant in that country it is such a typically arctic species that its occurrence in a fossil condition has often been held to denote that the deposit in which it occurs has been laid down during

an arctic climate. Yet the Irish climate, especially along the west coast, is so mild that some plants of a sub-tropical nature, such as the New Zealand tree fern, can be successfully reared in sheltered spots in the open.

I only mention these facts in order to show that too much reliance is apt to be placed on the importance of fossil plants as tests of climate.

As for animals and their dependence upon climatic conditions, I might give as an instance the Asiatic tiger (*Felis tigris*). It is an animal which we usually connect with a tropical climate, and which has yet adapted itself to the most arctic temperature known, as it inhabits both Siberia and India.

After these preliminary remarks, I propose to dwell a little while upon the writings of those who have given the subject of our own fauna and its geological history some attention.

I am commencing with the British and Irish fauna, that is to say, with the fauna of the British Islands, because it discloses, as it were, the key to the larger general European problem.

The first essay which has been published on the origin of the existing fauna of the British Isles was a very remarkable one. It was written in the year 1846 by the late Professor Edward Forbes, and well deserves the name of a classic. The author's studies led him to believe that the great mass of the animals and plants inhabiting our area had come from the neighbouring continent previous to the isolation of the islands. As regards the plants, Professor Forbes stated that "the vegetation of the British Islands presents a union of five well-marked floras, four of which are restricted to definite provinces, whilst the fifth, besides exclusively claiming a great part of the area, tends to overspread and commingle with the others."¹

On the accompanying map (Fig. 3), copied from Professor Forbes's paper, those five provinces are roughly indicated. They convey his idea at a glance.

It may be mentioned that, before Forbes, Mr. H. C. Watson had already conceived the idea of dividing Great Britain into a number of provinces illustrating the assemblages of particular

¹ Essay, p. 4.

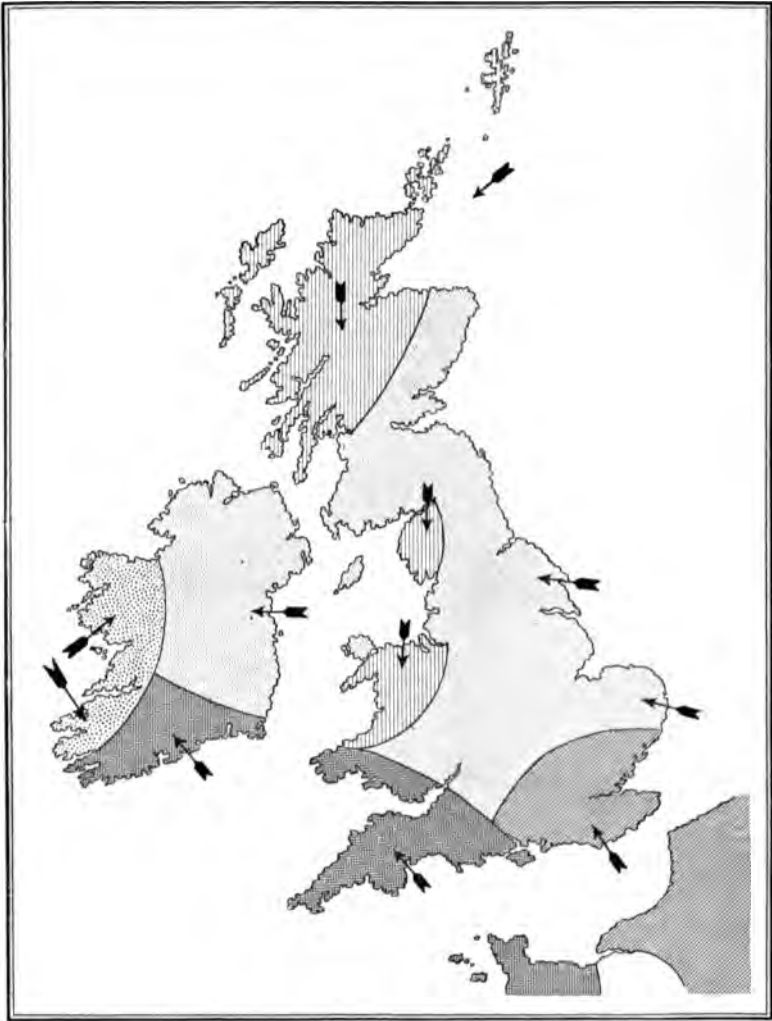
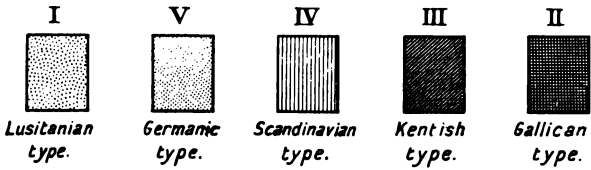


FIG. 3.—MAP OF THE BRITISH ISLANDS INDICATING THE FLORAL DIVISIONS AFTER E. FORBES. *By permission of H. M. Stationery Office.*



types of plants in the different districts. But Watson did not take into consideration the origin of these plants, nor did he show that the animal groups corresponded with the plant groups, as Forbes did. Forbes, for instance, included among the fifth group, which he called the Germanic, such species of animals as the mole, the dormouse, the polecat and the English hare, which, as he remarks, are all confined to the English side of St. George's Channel and become scarcer as we go northward.

Taking for granted that the animals and plants reached Great Britain by land, when it was connected with the continent of Europe, Professor Forbes argued that we still have to determine the "how and when" of the peculiarities in the British fauna and flora. We have "to ascertain two fixed points in time, between which the migration or migrations must have taken place."¹

The one fixed point he thought was the Eocene period, the other the historical—that is to say, the time during which man has been a known inhabitant of the earth. Some time between these two periods the migrations to this country must have taken place.

The principal conclusions Professor Forbes arrived at were that the various groups of animals and plants now found in the British Islands did not make their appearance there simultaneously, but at several distinct periods, and that they travelled over a continuous land surface from the Continent before, during and after the Glacial period. He also maintained that the Germanic fauna and flora, the fifth group, came to us after the Glacial period. He urged that the fourth or Scandinavian group arrived during the Glacial period, and that the third and second, which he called the Kentish and Devon or Gallican groups, are pre-Glacial in origin. Finally, he suggested that towards the close of the Miocene period the first group must have found its way to the south-west of Ireland from the north of Spain by means of a direct bridge of land, which, as he supposed, connected these two countries.

The great merit of Forbes's speculations lies in the fact that he has laid the foundations of a new method of research, which has

¹ Essay, p. 9.

been successfully adopted since by many botanists and zoologists in unravelling the problems of the origin of our flora and fauna.

Many years elapsed during which no attempt was made to follow up the interesting studies commenced by Professor Forbes. Many valuable monographs were published on several of the orders and classes of the animal kingdom, indicating their geographical distribution in the British Islands. But the authors did not endeavour to account for the causes of this geographical distribution. Among the earlier of these may be mentioned the essay on the geographical range of the butterflies in Great Britain by T. Boyd and A. G. More, and on the distribution of birds in Great Britain by the latter author. These followed closely on the lines laid down by Mr. H. C. Watson, and merely dealt with the grouping of types, not with their origin.

It was not until twenty-seven years after the appearance of Forbes's inspiring essay that the subject was once more brought under public notice by the publication of Mr. Birchall's little pamphlet on the origin and distribution of the insects of the British Isles. In referring to several species of moths found in the western districts of Ireland, he alluded to their being remnants of an ancient Mediterranean fauna. He also pointed out that a small number of moths had reached our shores from Scandinavia and Iceland. He did not, however, recognise Forbes's Kentish and Gallican faunas.

A few years later, a Scottish entomologist, Dr. Buchanan White, approached the subject of the origin of the mountain Lepidoptera of the British Isles, and investigated the cause of their peculiar distribution. About fifteen species of our butterflies and moths, he says, can be regarded as typical mountain forms, since they do not as a rule descend below 1,500 feet above sea level. Our mountain species of both animals and plants, he supposes, came from the south and followed closely upon the heels of the retreating ice at the close of the Glacial period. They thus found their way to Scotland, where most of them now occur. A few of them wandered from there to Ireland.

In a more recent essay, Dr. White discussed the wider problem of the origin of the British butterflies and moths as a

whole. He came to the conclusion that they reached our shores by travelling across the dry bed of the German Ocean, from continental Europe, after the Glacial period. The most widely distributed species he regards as the most ancient. Though part of the fauna of Ireland, he thought, came there by way of Scotland, he assumed that some of the butterflies probably entered our sister isle from the south.

Within recent years Mr. Kane reviewed the subject in a very thorough manner from an Irish point of view. He agrees with Dr. White in deriving the Irish butterflies and moths from a post-Glacial invasion, and suggests an ingenious explanation as to the method of migration of the peculiar western element by the assumption of a direct land bridge between Ireland and France unconnected with England.

The coleopterist has also dealt with the problem of the origin of the British fauna. Mr. W. E. Sharp claims that insects as a whole offer perhaps better and more cogent evidence, in an inquiry of this kind, than does any other class of our terrestrial fauna. For his special research he chose the beetles which seemed to him particularly suitable for the purpose. First of all he eliminated from the inquiry all those species which, although well established in this country, live under more or less unnatural conditions and depend for their continued existence on an environment caused by human agency.

The great bulk of our beetle fauna remains to be considered. And this, Mr. Sharp assumes, is genuinely indigenous and has established itself by direct migration from the Continent over a former land connection which joined the latter with England. He divides all these beetles into two great groups, which he calls "the adaptables" and "the non-adaptables," or progressives and conservatives. He implies by these terms that one group of beetles is able to adapt itself to the ever-changing environment; the other is not. The adaptable ones or progressives, he thinks, on account of their facility in establishing themselves in every portion of the country, are not of the slightest use to us in our search for the causes and methods of their original dispersal. Mr. Sharp eliminates therefore, besides the introduced beetles,

these progressive, ubiquitous ones. Those that finally remain, he considers, can be readily arranged into three or possibly four separate groups: first, the beetles confined principally to the highlands and moors of Scotland and Ireland; secondly, those which have their headquarters in England, forming an area of greatest density in the south-east, and thinning out north and westward, till the species become rare and in many cases entirely absent from Scotland and Ireland. The third group comprises all those species whose distribution is exclusively southern or south-eastern, and is often marked by extreme discontinuity in its range; finally, there is a small assemblage of species which either occur only in Ireland or which are found in England only in the extreme south-west.

The conclusions Mr. Sharp arrived at as the results of his studies are, that the first or Arctic element is distinctly older than the second, and that it reached us before the Glacial period from Greenland and North America. The second group he thinks came from the East, when the German Ocean was dry land, after the Glacial period, and with it the third group.

Mr. Sharp does not commit himself as to any definite view with regard to the age of the fourth group. He admits, however, that it could not have been derived from the East, and he suggests that it might represent the survivals of some lost Atlantis long sunk beneath the waves of the western ocean.

Messrs. Kennard and Woodward in their essay on the post-Pliocene non-marine mollusca of the south of England and Mr. J. W. Taylor have investigated the same subject from the standpoint of the conchologist. I have likewise indicated my views in a paper on the origin of the Irish land and fresh-water fauna and in other writings. They agree with those of the first-named authors in so far as we recognise that most of our species have reached this country from more than two sources, and that the Lusitanian element is one of the oldest we possess.

Mr. Taylor perceives but two elements, a western and an eastern one. The latter originated in the north European plain, and is steadily displacing the weaker western element in our fauna.

Lest there should be any misconception about the words "migrations," "wanderings," and "dispersals," which occur so frequently in the various authors' remarks just quoted, I should mention that these terms apply to the race, not the individual.

Species like swallows, locusts, or lemmings, do habitually undertake great migrations, but these are very exceptional in the animal kingdom. The rule is that animals stay at home and only migrate or wander in search of food within a small area.

Let me illustrate what I mean by an example.

The "homing instinct," or the faculty of returning to the same spot habitually, is possessed even by invertebrates of low mental capacity. When a slug comes out at night to forage for food, it generally returns to its shelter before the break of dawn. It has been observed that it does not travel back the same way it started, but generally describes a wide circle during its peregrinations. Very frequently it deposits its eggs in a convenient spot near the food it has discovered. When the young slugs emerge from these eggs they radiate or disperse from this new centre in all directions until they find a new shelter where they may pass the day in safety.

In this manner the individual area of the slug's range is not increased, but the race or species by slow degrees gradually gains territory, and that is what we understand generally by the words "dispersal," "wandering," or "migration," though it would seem desirable to restrict the latter term to such periodic movements in search of distant breeding places, as for instance, those of the swallow and other birds.

In the more intellectually endowed vertebrates, the homing instinct, or as we may call it, the love of home, has generally developed to a much higher degree.

After this short digression let us return again to our original theme. Professor James Geikie does not accept Forbes' interpretation to account for the presence in our area of the five elements recognised by him. The only flora, he thinks, which could possibly have outlived the Ice Age in Britain, would be

the High Alpine or Scandinavian. He assumes that during the Ice Age the climate in this country was arctic in severity, with the result that the fauna was practically exterminated. Professor Geikie accounts for the origin of our floral elements in the following manner. When the climate, after the Ice Age, became once more less arctic, the Scandinavian flora advanced northward from France, where it had previously been driven. It then spread over the British Islands, but, Ireland being now unconnected with Great Britain, the flora failed to cross the Irish Sea. "By-and-by, however," he continues, "the Irish Sea gradually disappeared, and a land connection took place between Scotland and Ireland, across which the alpine and sub-alpine flora and the reindeer would migrate." A more general elevation of the land, accompanied by a climate milder than the present, followed; and it was during this stage, according to Professor Geikie, that the Lusitanian plants found their way into the south and west of Ireland.

In accounting for the origin of our fauna, Professor Geikie assumes that the British Islands were connected with one another and with the Continent after the Glacial period, and that the climate became milder. But his opinion is not shared by geologists generally.

Professor Geikie does not allude to the very striking peculiarity shown by our arctic and southern plants and animals in so far as they exhibit discontinuity of distribution, while the great bulk of evidently more modern temperate forms have an almost continuous range.

Mr. Andrew Murray went much further than Professor Geikie in his conception of the severity of the Pleistocene climate. He believed that the pre-glacial fauna and flora were practically exterminated all over Europe.

When we reflect upon the various opinions expressed on the origin of our fauna by the authors I have referred to, there is one circumstance which must forcibly impress itself on our minds. While some started with the assumption that all life on our islands had been apparently exterminated by the climatic effects of the Glacial period, others,

including myself, had treated that important event in our geological history as a negligible quantity. As long as such extreme difference of opinion exists as to the real climatic condition of that period, as long as geologists are still in doubt whether part of our boulder clay is not a marine deposit rather than a terrestrial one, and whether the Ice age was divided by a warm interglacial stage or not, I think we are justified in dealing with the problem of the origin of our fauna from an independent standpoint.

For inspiration in this dilemma we naturally turn to Wallace's great works on the geographical distribution of animals. But while he discusses the problem of our fauna in his well-known books, he does not seem to have devoted much thought or study to it, as he dismisses the subject with few remarks. He holds of course that our fauna has travelled from the Continent across a former land connection in comparatively recent geological times. His latest views, as expressed in "Island Life," are that a considerable portion, if not the entire area, of the British Isles had been submerged during the latter part of the Glacial period to a depth of nearly 2,000 feet. This submergence, he thinks, must have destroyed the greater part of the life of our country. "We know," he continues, "that just before and during the Glacial period we possessed a fauna almost or quite identical with that of the adjacent parts of the Continent, and equally rich in species. The submergence destroyed this fauna, and the permanent change of climate on the passing away of the glacial conditions appears to have led to the extinction or migration of many species in the adjacent continental areas, where they were succeeded by the assemblage of animals now occupying central Europe. When England became continental, these entered our country; but sufficient time does not seem to have elapsed for the migration to have been completed before subsidence again occurred, cutting off the further influx of purely terrestrial animals, and leaving us without the number of species which our favourable climate and varied surface entitle us to."¹

¹ *Island Life*, p. 338.

Dr. Wallace does not in these statements offer any true explanation of the origin of our various faunal elements. For our fauna is not merely an impoverished counterpart of the French or German one. Nor does he venture to enlarge upon any speculation as to the respective ages of these groups, for it must seem evident that our South European animals cannot have entered the British Islands simultaneously with the mountain species of which Dr. Buchanan White has given us an account.

I need not dwell upon Professor Boyd Dawkins's views, as they resemble Dr. Wallace's in their main points.

Both Dr. Wallace and Professor Dawkins seem convinced that the Glacial period had a destructive effect upon the British fauna, though they attribute the destruction to water rather than climate. Formerly, indeed, it was currently believed that a large portion of Northern Europe was flooded by the sea during the Glacial period, and that icebergs floated in its waters. The boulder clay, which covers such extensive tracts in this country and in Northern Continental Europe, was held to be a marine deposit. Most geologists have now abandoned what we might call the aqueous theory, and have adopted another, according to which the boulder clay is the mud that collected under huge glaciers. It is evident that glaciers several thousand feet thick, if they existed in this country, must have had a chilling effect on the fauna and flora.

I do not wish to deal here with either the aqueous theory, of which Sir Henry Howorth is such an able champion, or with the terrestrial hypothesis, of which Professor James Geikie is the strongest representative. Both have embodied their opinions in well-known works, which may be consulted by those interested in the subject.

As for the past mammalian fauna which Professor Dawkins has made his special study, he was the first to draw attention to the remarkable commingling in early glacial deposits of southern species, which had survived from Pliocene times, and of such which had apparently arrived recently from Asia. From this fact he concluded that a vast migration of animals had set in

from Asia in Pleistocene times (Fig. 4) analogous in every respect to that by which European peoples arrived at their present

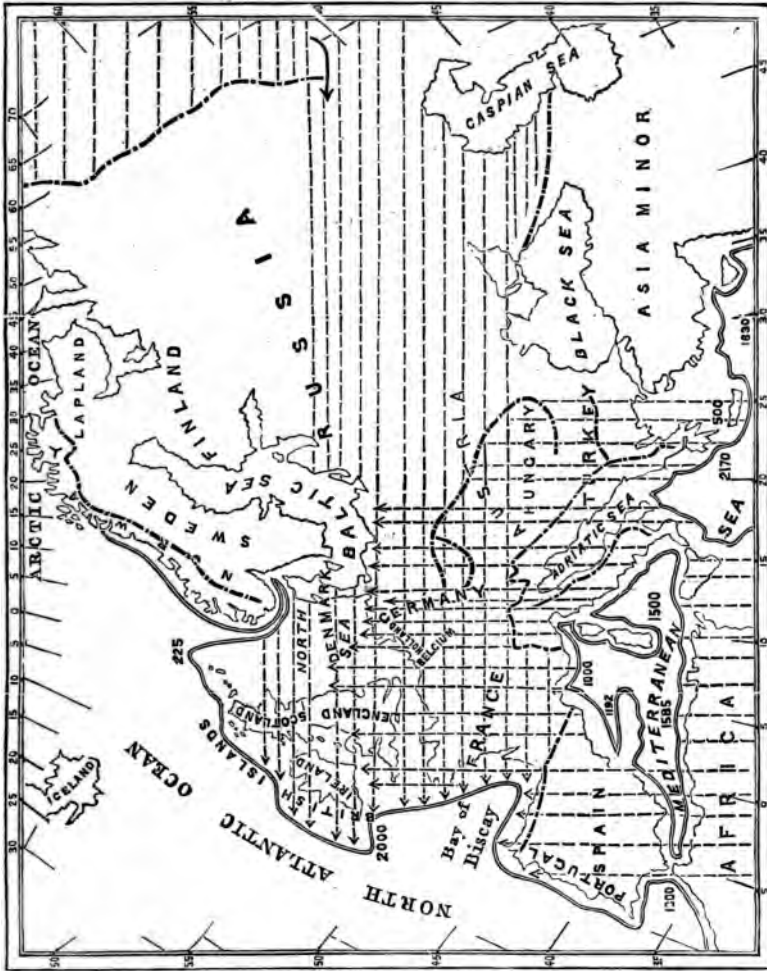


FIG. 4.—PLEISTOCENE EUROPE, SHOWING RANGE OF NORTHERN AND SOUTHERN MAMMALS. (From Prof. Boyd Dawkins's "Early Man in Britain," by permission of Messrs. Macmillan & Co.)

homes, and following for the most part the same route, between the Caspian Sea and the Ural Mountains. How are we to explain such an extraordinary mingling of southern and northern

species in the same deposit? Professor Dawkins assumed that the summers in Britain, when these animals arrived, must have been warm, as perhaps in Middle Asia, and the winters cold. In the summer-time the southern species would thus have wandered northward. When the cold winters came the northern species would occupy the area vacated by the southern animals.

However ingenious Professor Dawkins's explanation may be, the occurrence of the hippopotamus in the Pleistocene deposits of Yorkshire is very difficult to reconcile with such a seasonal migration hypothesis. Another aspect of the problem has also led Professor James Geikie to reject the explanation. As he justly remarks, such a supposition as the migration of a hippopotamus from Northern England to Southern France on the approach of winter cannot be maintained. He himself felt inclined to explain the anomalous commingling of northern, southern, and temperate forms, which so often occurs, not only in English deposits, but also on the Continent, by the supposition that very gradual changes in the climate took place during a long course of time. He favours, therefore, the gradual permanent departure of one fauna while it was being replaced by another.

Sometimes the remains of the southern mammals are in deposits distinct from those of a northern character, but recently Mr. Lydekker, in his handbook of the British mammalia, has again drawn attention to the fact, already alluded to by Buckland and others, that the remains of both tropical and arctic mammals have been found lying side by side in the same bed. His hint that we have yet to learn a good deal about the effects of climate on animals is very opportune. In Dublin we have kept lions successfully in the open air summer and winter for years, and they have even reared their young in an unheated shelter. An allied species, the tiger, which is often looked upon as a typically tropical species, ranges, as already stated, far north into Northern Asia, and there flourishes under intensely arctic conditions.

The methods I propose to adopt in elucidating the geological

history of our fauna as a preliminary to that of the fauna of Europe generally are simple enough. I intend first to describe some of the characteristic animals of the various groups or component elements of our fauna. By means of their general geographical distribution we shall then endeavour to trace the original homes of these animals. This will enable us to find out from what direction they reached our territory.

Dr. Wallace was perfectly justified in assuming that the absence of so many of our common English animals from Ireland indicated that the land connection between the two islands had already disappeared when England was still joined to the Continent. The Irish absentees will therefore furnish us with a date for our geological history. The geographical distribution of the recently extinct species will help to fill up gaps in our survey, and so little by little we enlarge our field of vision into the past.

There is one more subject which I should like to mention before concluding this chapter. How can we determine the original home of a species? It must be clear to every one that, as a general rule, an animal such as the badger (*Meles taxus*), for instance, must have arisen in one small area of the world, from which it has spread to others where we find it to-day. This area we may call its original home or the cradle of the species.

A species must tend to spread from its original home in all directions until it encounters some insurmountable barrier or obstacle.

An animal like the badger (Fig. 5), which can adapt itself to such extremes of climate as are present in Scandinavia and Spain, or Ireland and Greece, will not find many obstacles except an ocean to hinder its advance. We should expect its original home, therefore, to be somewhere near the centre of its geographical range.

The genus to which the various species of badger belong is only found fossil or recent in Europe and Asia. Hence there is no reason to suppose that it could have originated anywhere but in either of these two Continents. The most ancient fossil

remains of badgers occur in the Miocene of Persia, which country is situated approximately near the centre of its range. We can safely assume, therefore, that the badger originated somewhere in Western or Middle Asia, and trace from there its gradual peregrinations to other parts of the world.

Our fossil evidence is of so very fragmentary a character, that it is often extremely difficult to point to any particular



FIG. 5.—BADGERS (*Meles taxus*). PHOTOGRAPHED FROM A LIFE-GROUP IN THE BRITISH MUSEUM (*Nat. Hist.*).

country as the home of a species or genus. The present distribution, however, may be looked upon as a reliable guide in directing our inquiries in this respect.

Let us take as an example another familiar species, the stoat (*Putorius erminea*). The genus *Putorius* is quite absent from Australia, and from at any rate the central and southern portions of Africa and South America. There are altogether about forty-six species known to science. Only one of these penetrates into Northern Africa, one other has wandered into

Southern Asia and some of the great islands of the Malay Archipelago, five more have found their way into South America as far south as Peru, while another occurs in Central America. The remaining thirty-eight species are confined to North America, Central and Northern Asia, and Europe. No fossil forms are found beyond that area, while the oldest stoat-like species has been met with in the Miocene of France. We know practically nothing of the fossil mammalia of Central and Northern Asia, but, to judge from the recent range of the species, the home of the genus *Putorius* is more likely to have been there than in Europe.

There are in England four different kinds of the small turret-shaped snails, called *Clausilia*, which live chiefly in the crevices of old walls and under stones. When we cross over to Ireland, only two of them are met with. On the other hand, when we proceed eastward to Germany, we are able to collect sixty different kinds of *Clausilia*, in the Austrian dominions about one hundred and fifty. Still further south, in the Balkan peninsula, the number diminishes again. About one hundred and thirty species of *Clausilia* occur there, while beyond that, in Asia Minor, only about fifty have been found (Fig. 66). We may regard South-eastern Europe therefore as the cradle of the genus as far as Europe is concerned. There the conditions for the production of new species of *Clausilia* are apparently most favourable, and from this centre the species seem persistently to radiate outward to populate the surrounding countries.

CHAPTER II.

I EXPLAINED in the last chapter the course which has been adopted in tracing the past dispersals of animals from their original homes to the British Islands. This method was initiated by the distinguished naturalist Edward Forbes, the founder of the practical applications of the science of geographical distribution of animals. From year to year, as the knowledge of the distribution of the European animals becomes better known, the geological history of animal dispersals can be worked out with greater precision and accuracy.

I propose in this chapter to take into consideration the fauna of Ireland, which presents a somewhat simpler problem than that of Great Britain.

In Lough Neagh, the largest of our fresh water lakes, occurs a fish about the size of a herring, called pollan (*Coregonus pollan*). It also inhabits Lough Erne, Lough Derg and the upper parts of the River Shannon.

In the north of England, in the Lake District, two very closely allied species are met with, known as the vendace and the gwyniad. Both species also inhabit the south-west of Scotland, while the gwyniad has been taken in a small mountain lake in Wales. All the British lakes in which these fish of the genus *Coregonus* occur communicate with the Irish Sea, and it is probable that the Irish lakes alluded to, did so in former times.

The geographical distribution of these three species of fresh water fishes in the British Islands is so peculiar that one cannot help wondering how it could possibly have been brought about under the existing conditions of land and water. If, however, we imagine the whole of North-western Europe to be raised by a few hundred feet, the Irish Sea would become mostly dry

land. . A deep valley would remain in the middle of the Irish Sea which would become filled with water from the rivers of North-western England and from Eastern Ireland and form a great lake. Under such geographical conditions the present range of the pollan and its allies seems quite easily understood (Fig. 6).

If we suppose the common ancestor of the three species, the pollan, vendace and gwyniad, to have lived in that lake, it is perfectly conceivable that when the lake area was subsequently invaded by the sea from the south, our *Coregonus* ancestor would have migrated up the rivers and settled down in the smaller lakes connected with them. In the course of time the original species would have become modified and have formed the three closely allied species referred to.

We must look upon the genus *Coregonus* as of northern origin. Only one fossil form has been met with, viz., in the Pleistocene deposits of Sweden, and the genus has at present an essentially northern range. A few species have apparently ascended the great Continental rivers and established themselves in the northern lakes of Switzerland, but no *Coregonus* occurs further south. The genus is not altogether confined to fresh water; a few species migrate to the sea, like the salmon. The geographical distribution extends over Northern Europe, Asia and America.

It is of interest to note that the pollan, which I referred to as occurring in Lough Neagh, lives there on a fresh water shrimp known as *Mysis relicta* (Fig. 49). This shrimp is not found elsewhere in the British Islands except in Lough Erne in Ireland. All round the Baltic, in the lakes of Scandinavia, in Northern Russia and Northern Germany, as well as in the great lakes of North America, it reappears again. It is closely related to another shrimp (*Mysis oculata*) which only lives in the sea. Our fresh water species is supposed to have originated from this marine form. This supposition is rendered probable from the fact that almost all other species of *Mysis* inhabit the sea.

Many of the lakes referred to are inhabited by other species of invertebrates, whose relations are marine forms. Such fresh



FIG. 6.—MAP OF THE PROBABLE FORMER CONDITIONS OF LAND AND WATER OF THE BRITISH ISLES AND THEIR MARINE AREA AT A TIME WHEN THEY STOOD AT A HIGHER LEVEL THAN AT PRESENT.

water lakes are known by the name of Relict lakes, as I shall explain later on (p. 141), because they are supposed to have been flooded by, or to have been in close communication, with the sea at some former time. When the waters of the sea retired, some of the marine species are believed to have been left behind in the lakes and to have become somewhat modified in structure as the result of their transfer to another medium.

The fact that *Mysis relicta* occurs in these northern fresh water lakes and also in North America, and then reappears again in the Irish lakes, seems to suggest that it reached Ireland from the north-east.

Let us now take a survey of the fauna of Ireland as a whole. A visitor to the sister isle is at once struck by the absence of many kinds of animals and plants with which he is familiar from his country rambles in England. There are no moles in Ireland. None of the little rodents occur which occasionally injure the crops in the fields in England: I mean the voles; no snakes are met with, no blind-worms, and several of our common birds and fishes are absent. The entomologist misses many of his familiar friends in Ireland, while the conchologist will look in vain for the fresh water Unios and Paludinas or such large terrestrial species as the Roman snail (*Helix pomatia*), which is found commonly in the South of England.

Then again, if our visitor has purely sporting instincts, he will be surprised to meet with the Scottish highland hare in Ireland, both on the mountains and in plain, while he misses the English hare, which is absent. A naturalist who visits Ireland for the first time and extends his travels beyond the east coast of Ireland into the south-western or western parts, cannot help being astonished at the assemblage there of a set of plants some of which are cultivated in England as garden species and which there grow wild. And if he investigates the lower animals, he will meet with many strange forms which he never expected to find across the Irish Channel.

It is not correct, therefore, to speak of the Irish fauna as merely an impoverished British one. The Irish fauna, it is true, is characterised by the absence of many English species,



FIG. 7.—*ARBUTUS UNEDO*, WITH THE GEOGRAPHICAL DISTRIBUTION OF THE GENUS *ARBUTUS* IN THE

but also by the presence of many northern and southern forms of animal life which do not inhabit England.

Those who have travelled in the south of France or Spain



FIG. 8.—LONDON PRIDE (*Saxifraga umbrosa*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

have no doubt observed the evergreen Strawberry Tree (*Arbutus unedo*) (Fig. 7), which in sheltered situations in the southern counties of England is sometimes cultivated in gardens. As will be noticed by the range of this species, recorded on the

accompanying map, the only localities in the British Islands where this tree grows wild are in the counties of Cork and Kerry, in the south-west of Ireland.

A second species of *Arbutus* grows in South-eastern Europe—in Greece and on the islands of Crete and Rhodes. Altogether there are about ten different kinds of *Arbutus* known to science, all of which, except the two just referred to, are found in South America, Central America and parts of North America.

It seems strange that another typically Irish plant (*Saxifraga umbrosa*), which also occurs abroad only in South-western Europe, should have received the name of "London pride." This familiar plant, known among the Irish-speaking population as "good people's cabbage," grows only wild in the west of Ireland, the Pyrenees, and some portions of Spain and Portugal (Fig. 8).

In Connemara, in the west of Ireland, two kinds of heather grow in abundance, one of which has lovely bell-shaped flowers about half an inch in length. These are the Mediterranean Heath and St. Dabeoc's Heath. Neither of them are known elsewhere in our islands. They reappear again, however, on the Continent in the south of France, in Spain and Portugal.

There are many other plants included in this group.

When Forbes referred to these southern, or Lusitanian plants, as they have been called, he was quite unaware that there are a number of animals in Ireland which have a similar geographical distribution.

Hidden among the lichens which grow in such profusion on the rocks in Cork and Kerry, and scarcely distinguishable from them, there lives a beautifully spotted slug called *Geomalacus maculosus* (Fig. 28). It is unknown elsewhere in our islands, and on the Continent it occurs only in North-western Spain and Portugal, where several allied species are found.

Under stones, especially in the west of Ireland, we frequently meet with a millipede (*Polydesmus gallicus*), which at first sight resembles the common English species *Polydesmus complanatus*. It differs, however, from it in some important characters and does not apparently inhabit Great Britain. In France and

other southern countries it has been met with, and also in the Azores.

In the County Waterford and along the banks of the River Barrow a very shiny claret-coloured and extremely active woodlouse (*Trichoniscus vividus*) occurs, which, like the preceding species, is unknown in Great Britain. Even in France it has not been discovered further north than the Pyrenees, where we meet with it in abundance.

In Dublin and in the south of Ireland a large spider is frequently noticed which is distinct from the common house-spider (*Tegenaria domestica*). It has been named *Tegenaria hibernica*, though it is probably identical with *Tegenaria nervosa*, which inhabits the Pyrenees and Spain.

Among the beetles I might mention a large weevil (*Otiorhynchus auropunctatus*) not easily overlooked by collectors, which is abundant on the east coast of Ireland and has not been taken either in England or Scotland. Abroad it occurs in the Auvergne in France, as well as in the Pyrenees.

Finally there exists in Ireland a dragon-fly (*Tinodes maculicornis*) which has never been seen in Great Britain, while it is known from the south of France, Spain and Portugal.

These are some examples among a series of plants and animals, many of which are common in Ireland, while they are unknown elsewhere in the British Islands. What I have mentioned are only a small selection of species with a similar range, and many of these reappear again in South-western Europe. A geographical distribution of that kind is known as a "discontinuous" one. It has always been held to be a sign of great antiquity. The species probably spread originally along a former continuous coast line between France and Ireland. Owing to competition with better adapted forms or other unknown causes, they have, in course of time, become extinct in the intermediate tract, and are thus a standing testimony of an ancient origin.

There is good reason to believe that all the various animals and plants I have just referred to, and which form part of the Lusitanian group, originated in South-western Europe and

travelled northward at a time when the climate was milder than it is at present.

Another set of Irish animals and plants exhibit discontinuous distribution too, but they have evidently come to Ireland from the north.

We can recognise that this section is the result of two distinct dispersals, one being probably very much older than the other. In the older one we seem to be able to trace the remnants of a fauna and flora which once inhabited the ancient land which long ago must have stretched across the northern Atlantic region uniting the boreal districts of Europe and North America. I shall have occasion to refer again to this relationship in the European fauna with that of North America, when we come to the consideration of the animals of Scotland and particularly those of Scandinavia (p. 123). Many of these relicts of northern lands are confined in Ireland to isolated localities on the west coast. It seems almost as if they had been exterminated in their more eastern stations and had only been able to maintain themselves in the neighbourhood of the western mountains, which had perhaps afforded them shelter during the vicissitudes of past geographical changes in the distribution of land and water.

In some of the small lakes situated near the west coast of Ireland three fresh-water sponges have been discovered which are unknown in the rest of Europe. The only other region of the world in which they occur is North America. *Ephydatia crateriformis* was taken in a small lake in county Cork, *Heteromyenia Ryderi* in another in the county Kerry, while the third, called *Tubella pennsylvanica*, was met with in the north-west of Ireland. In America these species seem to be confined to the east coast.

No precisely similar geographical distribution of other fresh-water animals is known up to the present. But the European fresh-water pearl mussel (*Margaritana margaritifera*) evidently belongs to the same group. It is found in the United States, where other allied species exist. In Eastern Europe and Western Asia the genus is unknown. The pearl mussel is widely spread in

Western Europe, from Northern Scandinavia to Spain, without, however, entering a single river communicating directly with the Mediterranean or crossing the coast-line of that ancient

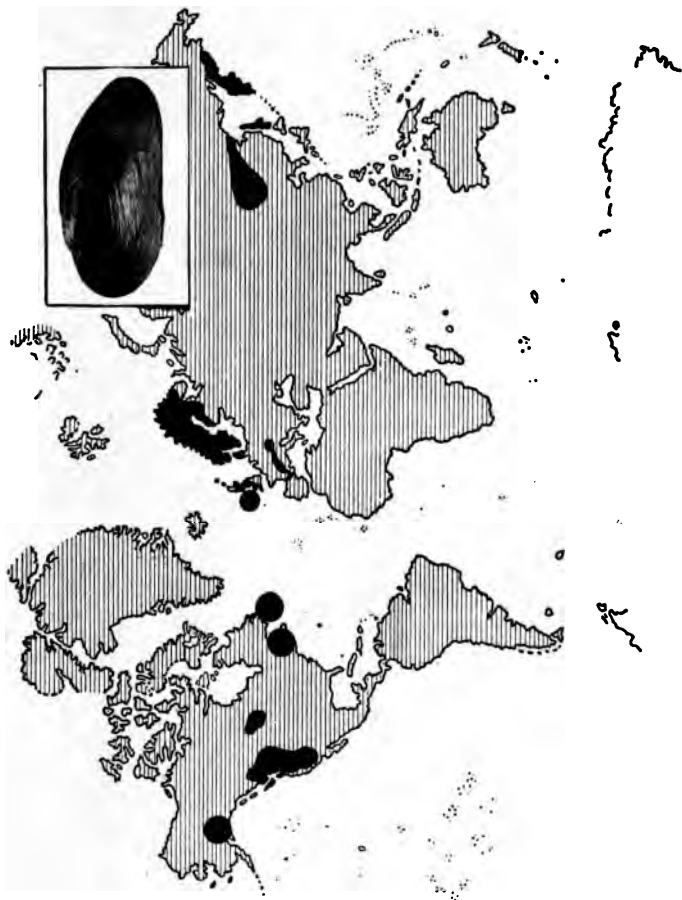


FIG. 9.—THE FRESH-WATER PEARL MUSSEL (*Margaritana margaritifera*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

Central European ocean which extended along the northern border of the European Alps eastward to Asia in Miocene times (Fig. 9). Its very discontinuous range, coupled with its peculiar European distribution and absence from Western Asia,

seem to imply that the fresh-water pearl mussel found its way across the Atlantic with the sponges just referred to at a very remote time.



FIG. 10.—THE SLENDER NAIAD (*Naius flexilis*). PHOTOGRAPHED FROM IRISH SPECIMENS IN THE DUBLIN MUSEUM.

Botanists have long been acquainted with other cases of distribution that can be matched with those of the Irish-American sponges. No doubt has ever been raised as to the claims of several species of American plants being indigenous to Ireland.

They reappear in North America, but are quite absent from the Continent of Europe.

Two of them are of exceptional interest, as they seem to confirm the view already expressed of the origin of the fresh-water animals referred to. One of them is the slender naiad (*Naias flexilis*) (Fig. 10). This water weed is found in two shallow lakes in the south-west of Ireland and in one in the County Galway. Both localities are in close proximity to the west coast. It has also been discovered in Perthshire and on the Island of Skye in Scotland. The other plant is the pipe-wort (*Eriocaulon septangulare*). Like most of the species referred to, it is met with chiefly in the south-west of Ireland, in lakes and bog pools near the sea, also farther north along the coast as far as Donegal. In Scotland it is absent from the mainland, but turns up again on the Islands of Skye and Coll off the west coast.

Finally, a beautiful orchid, which has received the name of "Irish lady's tresses" (*Spiranthes Romanzoffiana*), has been collected on the south-west coast and also in the north of Ireland, in the counties of Armagh and Londonderry.

The northern animals and plants I have described are manifestly the last lingering remnants of an ancient extensive fauna and flora. It seems as if we might add to them a very remarkable species of bird, with whose name every one is familiar, as it is one of those species which have become entirely extinct within quite recent times. I am alluding to the great auk (*Alca impennis*) (Fig. 11), which is considered such an adornment to a museum collection. The great auk lived in Scotland and Ireland less than a hundred years ago. To judge from the fact that its remains have been discovered in those refuse heaps of our ancestors called "kitchen middens" in the north and west of Scotland and in the north and south of Ireland, it was probably used as food by the early races of man in these islands. We have evidence of its occurrence on the coast of Durham and in Denmark. It probably lived in Scandinavia. In Iceland and Greenland it existed in great numbers, as it also did on Funk Island off the coast of



FIG. II.—THE GREAT AUK (*Alca impennis*), WITH THE GEOGRAPHICAL DISTRIBUTION. THE LITTLE AUK IS SHOWN FOR COMPARISON OF SIZE.

Newfoundland, so that its range extended in a semi-circle across the northern parts of the Atlantic Ocean.

There are a large number of other animals and plants in Ireland which, from the fact of their becoming scarcer as we proceed southward, and from their occurrence in Scotland and frequently far northward to the extreme limits of Arctic Europe, appear to have come from the north-east at a more recent period than these American forms.

Among them perhaps the most noteworthy is what is known in Ireland as the Irish hare (*Lepus timidus L.*), which however is only a variety of the Scottish and the Scandinavian or Arctic hare. This is the only hare found in Ireland, though both it and the English hare (*Lepus europæus*) inhabit Scotland. Moreover, in Ireland the Arctic hare lives in the plain as well as in the mountains, while in Scotland, and as a rule on the Continent, it is quite confined to the mountains, the other hare occupying the plain.

The general range of the Arctic hare—our Scottish and Irish hare—is of interest; especially in connection with its past range, it is distinctly instructive. It will be noticed by the map (Fig. 46) that it now inhabits the whole of the Arctic regions, certain isolated outposts further south, such as the high mountains in Japan, the Caucasus, the Tatra Mountains, the European Alps, the Pyrenees, Scotland and Ireland, all of which are far removed from its base or area of continuous range, which we must look upon as its original home. Three questions now arise which are of importance to our present inquiries, How did it reach these isolated localities, when, and why?

We conclude from the fact of no fossil remains of the Arctic hare having been found further south than the southern boundary of its present range and of the quantity of fossil remains increasing as we go north, that its original home was in the Arctic regions. What exactly was its geographical distribution in that area formerly we have no means of telling. Its southward movement must have taken place during recent geological times either in the Pleistocene or Pliocene periods, because we find remains of this hare abundantly in cave deposits,

some of which may be of Pliocene age, though they are commonly classed as belonging to the Pleistocene period. If we assume that the southward extension occurred in Pleistocene times, it seems probable that the Arctic hare originated in the Arctic regions in Pliocene or pre-Glacial times, that is to say before the Glacial period. So far the problem of the Arctic hare is simple enough. When we come to the question why did it leave its home to wander southward, we are confronted with a much more difficult problem, because it involves a consideration of the climatic conditions prevailing during the Glacial period, which is precisely one of the objects of this inquiry, but which I had thought of reserving for another occasion.

The great majority of geologists are of opinion, I think, that the southward extension of the Arctic hare and other northern forms of life, imply that the Arctic regions became uninhabitable for them, owing to the development of glaciers and the increasingly cold temperature on the advent of the Ice Age or Glacial period. On the return of more genial conditions, after the passing away of the Ice Age, the northern animals and plants are supposed to have returned north, leaving a few isolated colonies on the mountains, as a standing testimony of the rigorous climate in Europe prevalent during the Glacial period.

This seems a simple and satisfactory explanation of the present and past range of the Arctic hare. It does not, however, explain its occurrence in Ireland. If we argue that it was unable to depart from Ireland because the latter had become an island before the Arctic hare was aware of the fact, we have at once a ready interpretation of the reason why the Arctic hare should exist in Ireland, and also why the English hare should be absent there. The English hare was unable to reach Ireland because it entered England from the south, and found that Ireland had become a separate island. Everything points to the Arctic hare having been in possession of the British Islands before the other arrived.

There is yet another point which requires elucidation. At

the present day there occur irruptions or sudden invasions of one territory from another by hordes of certain species of mammals and birds. I have in my mind the well-known periodic movements of lemmings and of the sand-grouse, for example. Was the former occurrence of the Arctic hare in Middle Europe of that nature? or did it consist in a very gradual southward extension of its range? Our present experience of mammals and birds is that, whether a species suddenly invades another area from the one which it previously inhabited, or whether it gradually extends its range by the natural laws of dispersal, it does not become extinct in its original home. There seems to be a tendency to return to it after the wild rush for change. And all the members of the community do not participate in the exodus. A few stay behind, whose duty it appears to be to perpetuate the species in case the wanderers fail to return. We have to consider, therefore, whether the Arctic hare entirely left its original home, or whether, along with other Arctic species, it persisted and survived the Ice Age in the northern regions. This part of the problem I intend to discuss later on, when we come to deal with the Scandinavian fauna and flora.

Both the Scotch annulet (*Gnophos obfuscaria*) and the mountain rustic (*Agrotis hyperborea*), two small moths, have been observed on the west coast of Ireland and in Scotland: nowhere else in the British Islands. They appear to have entered Ireland from the north.

Similarly the running beetle, known as *Pelophila borealis* (Fig. 12) is widely distributed in the north of Ireland and on the west coast. In Scotland it only occurs in a few isolated localities as a great rarity. Further north it inhabits Scandinavia and Siberia. It is absent from the Central European plain and mountains.

Then there is a beautiful dragon-fly (*Somatochlora arctica*) found at Killarney. It only occurs elsewhere in the British Isles in Perthshire and Inverness-shire.

I might multiply these instances of species which, as far as Ireland is concerned, have a northern and western range, and

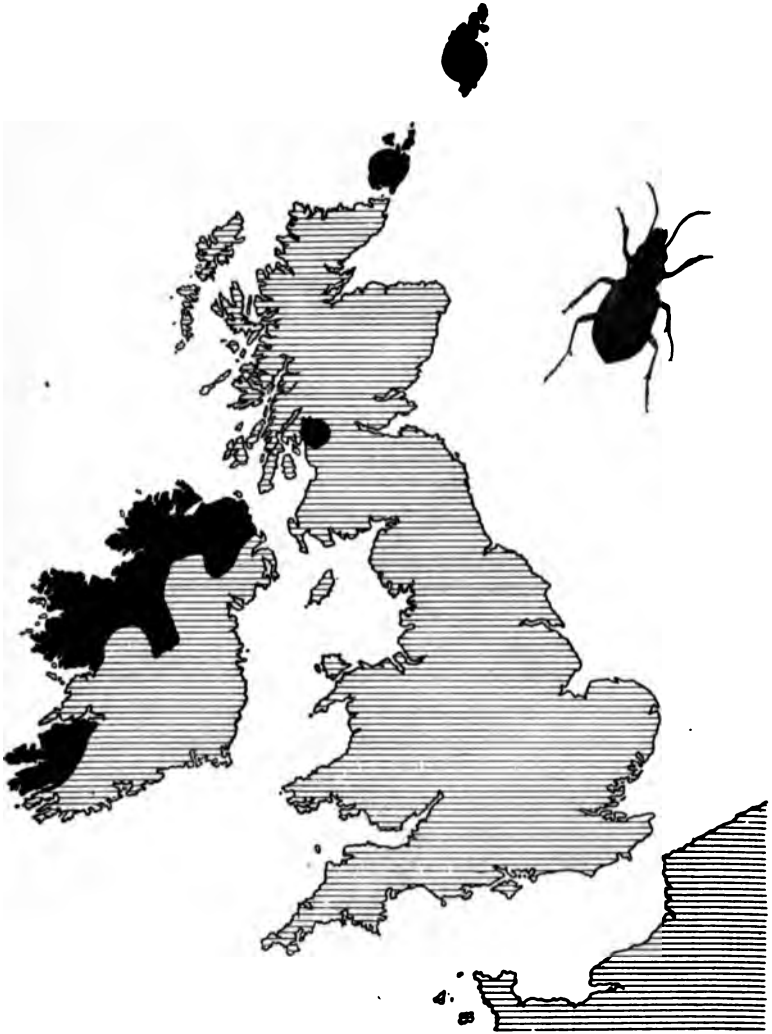


FIG. 12.—*PELOPHILA BOREALIS*, WITH ITS GEOGRAPHICAL DISTRIBUTION IN THE BRITISH ISLANDS.

thereby point to their having entered the island from the north. It might be objected that most of these are quickly moving species, that they might have settled down in a few suitable places, and that we cannot attempt to explain their course and direction of dispersal by their present range. But we can trace a precisely similar northern and western range in some of the slowly spreading snails, for instance, in *Arianta arbustorum* and *Clausilia laminata*, both of which are confined to the north and west of Ireland. Both of them also live in the highlands of Scotland. One of them, viz., *Arianta arbustorum* (Fig. 21), is obviously a more ancient species in Europe than the other, for it has succeeded in reaching the Orkney and Shetland Islands, and even Iceland. Altogether it has a much wider distribution on the Continent than *Cl. laminata*.

Among plants there are many belonging to this group, as, for example, the fringed sand-wort (*Arenaria ciliata*), which in the typical form occurs in the British Islands only in the west of Ireland.

In the case of the species just described, it seems as if they had originated in Scotland and spread southward from there into Ireland. But the continental range of many of the animals and plants belonging to this group enables us to conclude that such was really not always the case. The snails I mentioned are found in Ireland and Scotland, but also throughout England and Wales, and right across the plain of Continental Europe to the Alps. Owing to their greater adaptability to the vicissitudes of climate and food supply, the two species of snails still occur almost along the whole course of their former wanderings, while some of the others may have become extinct in England, and only persisted in the north and west of Ireland.

So far we have dealt almost exclusively with animals still living in the country. We have not taken into consideration those which inhabited Ireland in the past as revealed to us by the evidence of the cave deposits.

Quite a series of caves have now been explored in the north, west, and south of Ireland. They have yielded human remains

with many interesting implements of early man, and great quantities of bones of extinct animals.

Just as we have at present in Ireland animals and plants of a southern origin living side by side with those of a northern or sometimes Alpine origin, so it was in former times. In the Irish caves the bones of reindeer, Arctic fox, Arctic lemming occur together with those of African wild cat, brown bear, Irish elk, and wild boar, which must be looked upon as of southern origin. Again, the remains of Irish elk and reindeer have been discovered resting side by side in the marl deposits which usually underly the extensive bogs of the country. These marls are probably of more recent origin than many of the cave deposits in which the two deer occur together. In all likelihood the latter inhabited the country simultaneously for a considerable time. The fresh-water shells found in these marls are identical with those living in Ireland at the present day. And so far there is nothing to indicate that the climate during the marl epoch or during the cave epoch was colder than it is at present. All the mammals referred to are now extinct in Ireland, with the possible exception of the African wild cat, which may still be lurking in some of the more remote parts of the west, as I ventured to suggest in a recent paper.

Only one of them has become extinct altogether. Of the remainder, the reindeer, Arctic fox and lemming have withdrawn to their original northern home, from which they spread southward in former times. The African wild cat, hyæna, (lately discovered by Mr. Ussher), brown bear, and the wild boar have left in the opposite direction towards the south, from which they invaded the British Islands. Along with these southern and northern forms, now extinct in Ireland, came others which have persisted to the present day. I have already mentioned the Arctic hare. We have fossil evidence that the red deer, the badger, the common fox, the marten, the field-mouse, and others lived with these extinct forms in Ireland. They no doubt accompanied the southern species in their northward invasion, and have remained in the country.

To summarise the results which we have gathered from

these investigations of the Irish fauna and flora, we have evidence of an assemblage of very ancient animals and plants almost entirely confined to the south-west and west of Ireland. These reached Ireland from the south-west of Europe along the west coast of France, at a time when there existed a continuous coast-line between that country and Ireland. We have also some evidence that about the same time an invasion of Ireland took place from the north. A few relicts of the animals and plants belonging to that early period are also found on the west coast of Ireland. When all these forms of life reached the country it is impossible to determine accurately, but we can perhaps come to a more definite conclusion after estimating the age of those species which are absent from Ireland.

It seems, then, that while Ireland received its present animal and plant population from the north and south it must have had an extensive land connection with Great Britain (Fig. 6). Ireland subsequently became slowly separated from Great Britain owing to the sea creeping up St. George's Channel (Fig. 13). Finally the two islands were only joined by a narrow isthmus in the north. It was probably then that the Arctic species entered Ireland from the north and mingled with such as had succeeded in traversing England from the south.

As Ireland was converted to an island after having been a peninsula of our Continent, the inference would seem natural that its climate became influenced thereby. This question of climate in Europe during the time when the northern species invaded western and southern Europe is one of the most interesting problems which naturalists have to solve. Most authorities who have written on the subject are agreed that the southward advance of the northern forms indicated the advent of a great lowering of our temperature. I have endeavoured to show that neither the recent nor the fossil fauna supports such a contention.

The land and fresh-water molluscs associated with the northern mammals in Irish and continental deposits as a rule still reside in the same districts where they are found fossil. They lend no support, therefore, to the theory so generally



FIG. 13.—MAP OF THE PROBABLE FORMER CONDITION OF LAND AND WATER OF THE BRITISH ISLANDS AT A TIME WHEN IRELAND WAS STILL CONNECTED WITH SCOTLAND.

accepted that the temperature was colder at the time stated than it is now.

The French botanist Saporta contended, indeed, from a study of the plants, that the climate of Europe during the Glacial period, at some distance from the glaciers, was milder, though more humid, than it is now. Tsherski, who is so well known from his studies of the Siberian fauna, came to similar conclusions.

I might mention that Prof. Penck urged that the perpetual snow line in Europe was then lowered by a thousand feet. From these arguments Prof. Brückner deduced that the mean temperature of Europe must have been only from three to four degrees lower than it is now. The belief, therefore, in such extremely arctic conditions as to destroy both fauna and flora in Northern Europe is not shared by all geologists.

Prof. de Lapparent reasoned that the Glacial period marks a stage in geological history when a considerable increase of atmospheric precipitation took place as the result of a series of subsidences in the northern Atlantic region. This moderate view of the case seems to me to agree best with the evidence derived from a general study of the European fauna.

CHAPTER III.

IN Scotland there exists, just as in Ireland and in England, a fauna composed of different elements. There are animals and also plants which certainly must have wandered north in the dim ages of the past from South-western Europe. They are not as abundant, though, as they are in Ireland. Their number greatly diminishes as we proceed northward. We also notice a few remnants of an American group. They likewise seem to diminish in number as compared with Ireland. The presence of Arctic or northern species, however, is a more salient character of Scotland than of Ireland; and many of the Germanic forms of animal life which abound in the plain of Europe, especially towards the east, penetrate far into Scotland, while they are absent from Ireland, showing clearly that they spread northward after the formation of the Irish Sea.

I will now refer to a few of the more important types of animals which illustrate the component elements in the Scottish fauna. Major Barrett-Hamilton has shown that on the west coast of Ireland, in the Outer Hebrides and on the Island of Skye, there exists a small dark-coloured field mouse which does not occur elsewhere in the British Islands or on the Continent except in Portugal. He named it *Mus sylvaticus celticus*. It probably came from South-western Europe. I do not wish to suggest that the field mouse originated in Portugal, but it may be that we have here the last representative of an ancient dark-coloured race which in other places has been superseded by the larger light-coloured one, which may be of more recent origin. The field mouse, no doubt, is one of the most ancient of our native mammals. It occurs in English Pliocene deposits such as the Forest Bed, and is met with abundantly in English and Irish caves associated with extinct mammals.

The natterjack toad (*Bufo calamita*) is scarcely known as a native of Scotland. In Ireland, too, I have often been assured that St. Patrick banished it, along with snakes and such-like venomous creatures. Yet this species does inhabit both countries, and it is undoubtedly of South-west European origin. Its discontinuous range bears the impress of its ancient origin.

In Ireland we meet with a very quaint-looking weevil (*Rhopalomesites Tardyi*) (Fig. 14) so commonly that it deserves to be classified among the Irish injurious insects. Yet in both England and Scotland it is one of the greatest rarities. The genus to which it belongs is known from the Mediterranean region and the Atlantic Islands. It may be grouped, therefore, among the Lusitanian species.

There are two different kinds of woodlice, which I may quote as examples of the same wave of dispersal that issued forth from the south-west of Europe. It is interesting also to note that they reach in Scotland their most northerly point of distribution in Europe.

The first of these (*Trichoniscus roseus*) is of a beautiful light vermilion colour with a pale yellow stripe down its back. It is quite a subterranean species. It has been taken in the south-west and west of England, in Ireland, and also near Tarbert on Loch Fyne in Scotland.

The other species (*Platyarthrus Hoffmansseggii*) (Fig. 1) is noteworthy from the fact that it is blind and that it spends its entire existence in the nests of ants. The latter probably employ it as a scavenger, but they do not carry it away with them when leaving their nest: at any rate it is not molested by the ants. It is a minute creature, perfectly white in colour. In Scotland it is only known from Banff and Fifeshire. It has a wide range in Ireland; in England it has been met with in the south only.

Two snails included among the same Lusitanian element show a somewhat more extended range. They agree with the woodlice just referred to in so far as that Scotland is the most northerly limit of their range in Europe.

Helicella acuta is very common in Ireland, while in Scotland



FIG. 14.—*RHOPALOMESITES TARDYI*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

it is confined to a few scattered localities in the west and north. In England it has a much wider range, yet it shares the peculiarity with all the other species of that southern assemblage in being more or less confined to the western counties.

Pupa anglica is confined to the south-west of Scotland. In England it is met with in the north and south-west, whilst in Ireland it has a wide range. Abroad it lives in the Pyrenees and in Portugal. Closely allied forms occur in Madeira.

Finally, I may refer to a most interesting species of fern, which lingers on in Scotland, Ireland and Wales in a very few localities as a relict of this same Lusitanian dispersal, namely the bristle fern (*Trichomanes radicans*) (Fig. 15), or Killarney fern, as it is called in Ireland. Abroad we have to go to Western Spain to find this tropical-looking plant. Still further west it grows on the island of Madeira, in the Azores, and in the Canary Islands. Crossing the great Atlantic, it turns up again in the West Indies and in South America. About eighty other species of these filmy ferns are known to science, almost all of them being confined to tropical countries.

The thirteen species of liver-worts, peculiar to the British Islands, all occur on the west coast, and all have their nearest relations in tropical or sub-tropical countries. This seems to show that at some remote geological period, when a much milder climate prevailed in Northern Europe than at present, they advanced northward and are the last remaining relicts of this modified tropical flora.

The next element in the Scottish fauna which we have to consider is the Western or American one, which I referred to (p. 34) as occurring in the west of Ireland. The fresh-water pearl mussel, so well known in Ireland, also inhabits Scotland, except the extreme north and the eastern lowlands.

The two plants *Eriocaulon septangulare* and *Naias flexilis* I have dealt with fully in the last chapter, and need not quote again, but I might add the quillwort *Isoetes lacustris*. The extinct bird, the great auk, seems to belong to the same American element in the Scottish fauna.

I have drawn attention to the fact that the species showing an Arctic or northern range are more abundant in Scotland



FIG. 15.—THE BRISTLE FERN (*Trichomanes radicans*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

than they are in Ireland. Thus the ptarmigan (*Lagopus mutus*) of Scotland is unknown in the rest of the British Isles, but

reappears again in the Alps, the Pyrenees and in Scandinavia. Later on, when we come to deal with the continental faunas, I may have to say a few words about its probable origin. The snow bunting (*Plectrophenax nivalis*) is a more typically Arctic species, since it is not known to breed further south than Scotland.



FIG. 16.—*ANARTA MELANOPA*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

Turning to the invertebrates, there are a number of strikingly arctic forms in Scotland. The broad-bordered white underwing (*Anarta melanopa*) (Fig. 16) has been taken in Perthshire and in the Shetland Isles. On the Continent it has been observed in Northern Scandinavia and the Alps.

Two handsome dragon-flies, *Æschna cærulea* and *Somatochlora*

metallica, are confined to Scotland, as far as the British Islands are concerned. The former is found in Scandinavia, the High Alps, the mountains of Silesia, and in Perthshire.

Among the beetles, I might mention the fresh-water species *Dytiscus lapponicus*. Like almost all the other ancient species, it is confined to a few localities on the west coast, and it has sent off-shoots into Northern Ireland. Abroad it is only known from Northern Europe.

Particularly conspicuous in Scotland is the Arctic flora, or Scandinavian type of vegetation, as it has been called. Professor Forbes long ago drew attention to it, and since that time many additional plants have been brought to light, forming part of this section of the British flora. Mr. Crombie alleged that there was a greater similarity between the British alpine and the Scandinavian floras than between those of any other countries. He asserted that it was evident that the latter flora could only have come to Scotland at a time when there was some connection between the mountains of Scandinavia and Britain, though he seemed to think there was no evidence for a continuous land-connection.

I shall return to this question of the former land-connection between Scotland and Scandinavia when we come to deal with the latter country (p. 126).

Among the most noteworthy species are the blue menziesia (*Menziesia cærulea*), the rock draba (*Draba hirta*), the Scottish primrose (*Primula scotica*), the Arctic saxifrage (*Saxifraga nivalis*). None of these grow on the European Alps. I might also mention two species, which form so conspicuous a feature in many Glacial deposits, namely, the dwarf birch (*Betula nana*) and the mountain avens (*Dryas octopetala*) (Fig. 2). Both of these still persist in Scotland. The latter is particularly interesting as throwing light on the possible origin of some of these plants, for it grows not only in high regions of the Alps and Asiatic mountains, but likewise flourishes, as already remarked, on the west coast of Ireland down to sea level, where it is under the influence of one of the most equable climates in Europe. It nestles there among the limestone crevices in the mild



FIG. 17.—RESTORATION OF THE IRISH ELK (*Cervus giganteus*). (After Keller-Andrae, by permission of Messrs. T. G. Fisher & Co.) THE APPROXIMATE AREAS IN WHICH ITS REMAINS HAVE BEEN FOUND ARE INDICATED IN BLACK.

atmosphere engendered by the proximity to the Gulf Stream, while in most of its other habitats it is buried in the snow for the greater part of the year. It seems to be equally at home in these two extremes of climate. Might it not have adopted the present Arctic habitat as a secondary one?

Before concluding with the northern element of the Scottish fauna and flora, the question suggests itself, What light does the extinct fauna of Scotland throw on the origin of the recent one?

As in Ireland, deposits of loam and marl often covered by peat beds are abundant. They mark ancient lake sites. In these lacustrine deposits have been discovered the remains of the Irish giant deer (*Cervus giganteus*) (Fig. 17), the reindeer (*Rangifer tarandus*), the moose deer (*Alces machlis*), the wild boar (*Sus scrofa*), and the beaver (*Castor fiber*), all of which are now extinct in the country, along with others, such as the roedeer (*Capreolus caprea*), which still inhabits Scotland at the present day.

Although we have here too a mixture of southern and northern types of animals, they are not quite the same as we have met in Ireland. The moose deer, roedeer and beaver did not apparently cross over to Ireland. We may presume therefore, with Alston, who made a special study of the Scottish mammals, that these three species only penetrated to Northern Britain after Ireland had become separated from Scotland.

Some of these Scottish lake deposits disclosed the remains of a small crustacean which, with its large dorsal shield, bears a certain superficial resemblance to the great king crab. This creature, known as *Lepidurus glacialis* (*Apus glacialis*) (Fig. 18), no longer inhabits Scotland. It is a typically Arctic species, being found in Norway, Lapland, Bear Island, Spitsbergen and Greenland, as well as in some parts of Siberia.

This brings us now to the consideration of the third element in the Scottish fauna, namely, the English, or what we had better call the Germanic group.

The beaver still existed within historic times in England and Scotland. It is now practically extinct in Western Europe. A

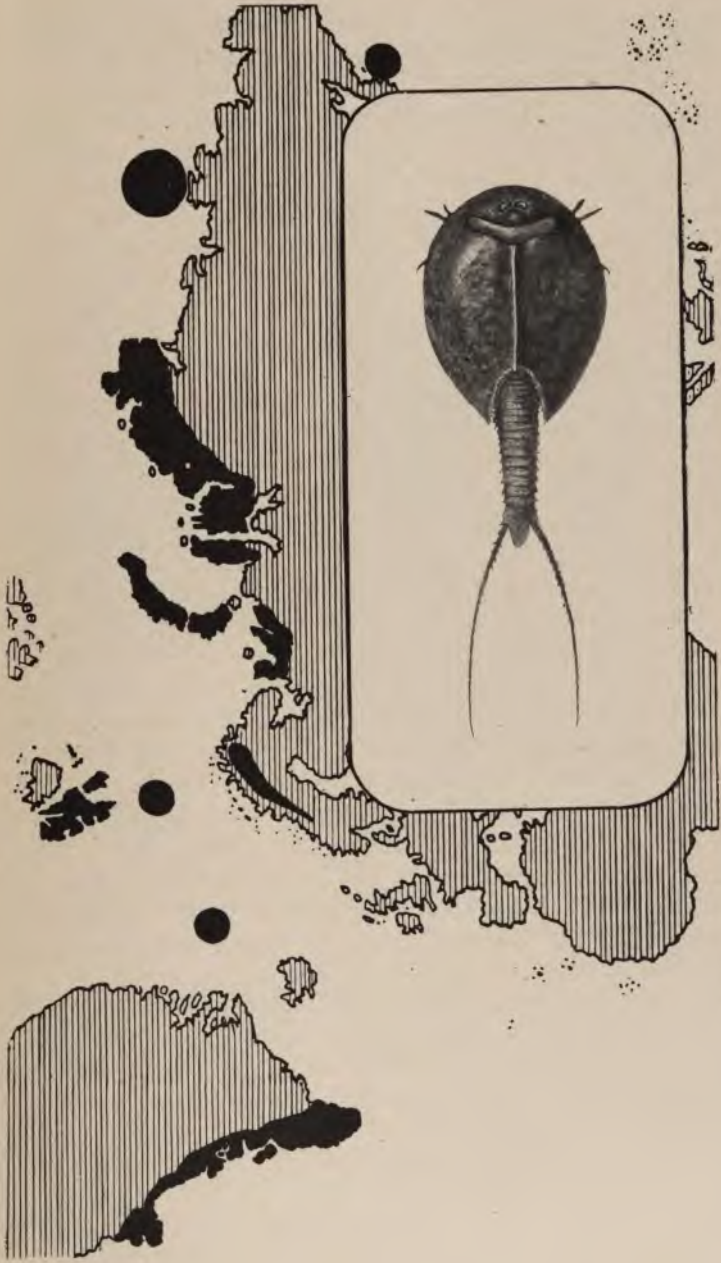


FIG. 18.—LEPIDURUS GLACIALIS, WITH ITS PRESENT GEOGRAPHICAL DISTRIBUTION.

few pairs still frequent the shores of the Rhône and the Elbe. Towards the east it becomes more abundant. In Russia and throughout Siberia it is still plentiful. We have here an example of an animal which evidently spread westward from the east, since it has never been found fossil in either Ireland, Italy or Spain, where we should expect it to occur if it had originated in the west. We shall become acquainted later on with numerous other examples of such Germanic animals whose past and present geographical distribution clearly indicate the manner in which they have advanced into Europe, and then extended their range from one part of our Continent to another.

The mole (*Talpa europæa*) (Fig. 19) is found throughout England, Wales and Scotland, but it is quite absent from Ireland. Now, if the mole had originated in Western Europe, we should expect to meet with it everywhere throughout Western and Southern Europe, since it inhabits almost the whole of Asia north of the Himalayan mountains, and has had ample time to spread. Such, however, is not the case. It occurs in Northern Spain, but has not travelled further south in the Spanish Peninsula. Its distribution in Italy is similar. Its range implies that it has succeeded in recent times in creeping round the base of the Alps into Lombardy, and similarly round the Pyrenees into Northern Spain. Further south it is unknown. Then, again, although the mole found its way into Scandinavia, it has not had time to conquer the extreme north. It is not the climate that keeps it back, for it accommodates itself to the greatest diversity of temperature and soil.

Like the beaver, the mole must have advanced westward from Asia into Europe apparently within comparatively recent geological times. So much we can argue from its present geographical range.

Now, it is interesting to note that the remains of both beaver and mole have been discovered in the newer Pliocene deposits of Norfolk, known as the "Forest Bed." By some geologists this Forest Bed is believed to belong to the lower Pleistocene series, rather than the Pliocene. It does not matter very much where we put it. The important point to remember is that it

is clearly older than the lower boulder clay. The two species, whose mode of dispersal is so distinct, dwelt therefore in



FIG. 19.—THE MOLE (*Talpa europaea*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

England before the deposition of boulder clay. Yet, although they were able to spread to Scotland, they did not penetrate to Ireland. It might be argued that possibly they did set foot in

Ireland, but became extinct there subsequently. If these two instances were isolated cases, such an argument might perhaps furnish an explanation of the facts of distribution. But when we find precisely similar examples of the absence of Germanic species from Ireland practically among all groups of animals, as we shall see later on; when botanists tell us that the most striking feature in the flora of Ireland is the extreme poverty there of the Germanic type of plants (which in their general range correspond to the animals I referred to), then we must acknowledge that this is no chance case of distribution. Plants as well as animals, paradoxical as it may seem, marched westward together, and it could only have been an almost insurmountable barrier, like a wide sea-channel, which was capable of arresting their further progress.

I need not dwell upon the origin of this Germanic section of the fauna any longer. I shall return to the subject and discuss it more fully in the next chapter, when I intend to summarise the results of our inquiries so far.

A third conspicuous mammal which is found in Scotland, and not in Ireland, is the roedeer (Fig. 20). At present this species still occurs sparingly in some of the northern counties of England, and we possess sufficient fossil evidence that it must have been abundant in this country not long ago. The destruction of the forests and the progressive cultivation of the land have no doubt been the principal causes of its extinction. Its European range corresponds closely with that of the two species just considered. As we might expect from its facilities for dispersal, it has gained possession of a rather wider area than the others in such countries as Spain and Italy. Yet it is absent from the extreme south of Europe and from the Mediterranean islands, as well as from Ireland.

The presence of roedeer remains in the Forest Bed is particularly significant, for it proves that this forest-loving species, whose westerly progress was not restrained by barriers which probably proved formidable obstacles to the beaver and mole, met with one which was insurmountable in the Irish Channel.

Ireland possesses only three kinds of amphibians, while there

are six indigenous to Great Britain. Let us take for example the newts. The three British newts all occur in Scotland. Only one, the smooth newt (*Molge vulgaris*), inhabits Ireland. The palmated newt (*Molge palmata*) has, like the last, a wide range in Scotland. The crested newt (*Molge cristata*) is rare and local, and is not found far north. It would appear, there-



FIG. 20.—THE ROEDEER (*Capreolus caprea*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

fore, as if the smooth newt was the first comer to the British Islands, and that the palmated newt came next, and finally the crested newt.

Extremely few fossil remains of newts are known; and strange to say, the only fossil British species which is known is the crested newt, a leg bone of which was disinterred from the Forest

Bed. The other two species of newts must consequently also have inhabited this country at that time or even earlier. At any rate the smooth newt, which has the widest range, must have lived in the British Isles since Pliocene times.

The general range abroad of the three newts is somewhat different from what we might expect, for the smooth newt and the crested newt are the two most widely spread newts in the Holarctic region. They range into Siberia, while the palmated newt is essentially a western form. Its centre of distribution is in France; from there it radiated forth into Great Britain, Northern Spain, and Western Germany.

We may explain the peculiar range of the three newts in the British Islands by the supposition that the smooth newt and the crested newt have originated at different times in Central or Eastern Europe. The palmated newt may be of more recent origin, but having had a shorter distance to travel, it would thus have invaded our area in advance of the crested newt. Another possible explanation of their anomalous distribution has yet to be considered. All the three species might have reached Ireland, two of them having since become extinct there; or they may still exist and have eluded the vigilant eye of the Irish naturalist.

The latter supposition is, I think, a very unlikely one, because I have had newts collected in all parts of Ireland for the past twenty years, and none but the smooth newt have ever been sent to me. The other view appears to me improbable, because the physical conditions, I mean the frequency of lakes and rivers, are most favourable to newts in Ireland.

The common frog (*Rana temporaria*) is present everywhere both in Great Britain and in Ireland. It has been argued by some naturalists that it was recently introduced into Ireland, but the fact that it is much more common in the west than in the east, and that it has been found in many of the recently explored caves from the lowest to the uppermost deposits, disposes of that tradition.

Of the two toads inhabiting Scotland, the natterjack (*Bufo calamita*) has already been referred to. It is a striking example

of discontinuous distribution. The common toad (*Bufo vulgaris*) is absent from Ireland, but common from the north of Scotland to the south of England. Its Continental range is enormously wide. It occurs everywhere between Japan and Gibraltar. It exists even in Marocco and Algeria. Its absence from Egypt and Syria points to its having crossed the Mediterranean from Europe by an old land-connection from either Sicily or Gibraltar. Hence it is possible that Ireland was already an island while North-western Africa was still joined with Southern Europe and thus received many members of our European fauna. Whether this was so we shall be able to judge better later on. Meanwhile it must be apparent how we may arrive at some estimate of the age of an island fauna even without utilising the remains of animals which have been preserved to us in geological deposits.

The fact that the blind-worm or slow-worm (*Anguis fragilis*) is found throughout Great Britain and not in Ireland has been alluded to.

Of the snakes, only the viper (*Pelias berus*) (Fig. 58) occurs in Scotland. It extends far north into the highlands. No snakes, as I have had occasion to mention, have ever been found in Ireland.

A very extensive list of the molluscs, spiders, insects, and other groups which exhibit a similar range to those which we have just reviewed, might be collated. But I think I have specified quite enough to demonstrate the manner in which the Scottish fauna approaches the English and differs from the Irish.

Before leaving the fauna of Scotland, a few remarks on the fauna and flora of the Orkney Islands, the Shetlands, and Farøes may be of interest. Iceland, too, will be included here as an extreme outlier of the North-west European fauna.

Of the Farøe Islands and Iceland, Professor James Geikie remarks that their plants are just such as ought to occur there if continuous, or nearly continuous, land had permitted their immigration. He believed that this land-connection had taken place subsequent to the Glacial period, because he

assumed the destruction of the flora during the Ice Age. A Danish botanist, Dr. Ostenfeld, recently made a renewed survey of the flora of the Farøe Islands and came practically to the same conclusion, namely, that the principal part, at any rate, of the plants inhabiting the islands had wandered across to them on a post-Glacial belt of land.

Out of 277 species of plants, he thinks not more than ninety-eight, that is to say, 35 per cent., might have been carried to the islands by the action of winds. The direction of the ocean currents is unfavourable to the occasional carriage of seeds by water. As regards the transport of seeds by birds, it appears that the flight of migratory birds across the Farøe islands is inconsiderable. The suggestion that birds during migration might carry seeds on their wings or feet to distant lands is not confirmed by actual observation. Many thousands of such birds have been carefully examined by Professor Winge and Dr. Knud Andersen, who noticed that their crops and stomachs were always empty. They never observed any seeds adhering to the feathers, beaks or feet of the birds. Dr. Andersen, moreover, is of opinion that migratory birds are scarcely of any importance as plant disseminators. The supposition of an ancient land-connection between the Farøes and North-western Europe is certainly supported by geological reasons. For there is a submarine ridge between the Shetland Islands, the Farøes and Iceland, from which the recently fitted-out Danish Ingolf Expedition dredged a number of shallow water shells.

As far as we are acquainted with the animal inhabitants of the Farøes, they contain forms of animal life that are widely spread in the British Islands, and of which we may reasonably suppose that they are very ancient members.

The animals of Iceland are far better known. The island being very extensive, it offers a wide field for a varied fauna. Besides the reindeer, supposed to have been introduced by man, the Arctic fox inhabits the island, and, in addition, one of the most widely spread and probably one of the most ancient mammals of Europe, namely, the field mouse (*cf.* p. 48).

Twenty-one different kinds of land and fresh water molluscs are known from Iceland, including well-known species such as *Arianta arbustorum* (Fig. 21). This is not likely to have been accidentally



FIG. 21.—*ARIANTA ARBUSTORUM*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

introduced, and its presence in Iceland strongly supports the idea of a former land-connection between that island and Europe. Such common European woodlice as *Porcellio scaber* and *Oniscus asellus* are liable to be unintentionally carried by

man. Yet the fact that these two species are widely spread and apparently indigenous both in Europe and North America, and are found not only in Iceland but also in the Faröes, is significant.

Among the Iceland fresh water molluscs there is one which has probably been derived from a former land-connection with Greenland, viz., *Succinea groenlandica* (Fig. 22). It is common to both countries, yet quite unknown in Europe proper.

While no less than thirty-three kinds of moths are known from Iceland, no butterflies have yet been discovered there. Among the moths there are several forms peculiar to the



FIG. 22.—*SUCCINEA GROENLANDICA*. PHOTOGRAPHED FROM SPECIMENS IN THE BRITISH MUSEUM (*Nat. Hist.*).

island, such as *Mimaescoptilus islandicus* and *Gelechia thuleella*. Some, like *Agrotis quadrangula* and *Hadena sommeri*, have apparently penetrated to Iceland from the New World, since they are only found in Arctic America, Greenland, and Iceland. Others that have come from Europe find in Iceland their most westerly limit. This is in perfect agreement with the distribution of the land and fresh water mollusca.

A small white bug (*Orthezia cataphracta*) which is extremely abundant in Greenland and Iceland is worthy of notice on account of its remarkable range. It occurs in Arctic America, in Siberia, and also in Lapland, the Faröe Islands, Scotland, the North of England, the West of Ireland, and again further south in the isolated "Riesengebirge" in Germany,

and in the Alps. As it lives under stones, it is not one of those insects that are transported accidentally; and it is another supporter, therefore, of an ancient land-connection between Europe and North America, by way of Iceland and Greenland, having formerly existed.

There are other hemiptera in Iceland, of which *Corixa carinata*—a fresh water species—deserves special mention. It has been met with in the Pyrenees, the Alps, the British Isles, the Faröes, Iceland and Scandinavia.

Other fresh water groups point to much the same conclusions. Some Arctic European forms of crustaceans, such as *Bosmina arctica* and *Diaptomus minutus*, have their most westerly extension of range in Iceland, while the North American *Diaptomus glacialis* is also known from Greenland and Iceland.

It is not possible here to discuss the Iceland flora in detail. There are two plants which are of particular distributional importance, and might be mentioned as examples of the two groups of distribution. These are the two orchids, *Habenaria hyperborea*, which ranges from North America to Greenland and Iceland, and *H. albida*, which occurs from the Urals in Eastern Europe to Arctic Europe, Scandinavia, the British Islands, the Faröes and Iceland.

In alluding to the north-western outliers of Europe, I almost omitted to mention the Orkney and Shetland Islands, which possess a comparatively richer fauna and flora than the remote island groups referred to.

The Orkney Islands are situated between the North of Scotland and the Shetlands. They can boast not only of possessing the common toad, but the pigmy shrew (*Sorex minutus*), and, what is most remarkable, a mammal quite distinct from any found on the mainland. This is a vole (*Microtus orcadensis*), and has only quite recently been identified as being distinct from the British vole (*M. agrestis*). It probably inhabits the Shetland Islands as well, for a vole is known to exist there.

It would appear, therefore, as if the voles of the *M. agrestis*

type had come to the British Islands in very early times, as they must have travelled to the extreme north at a time when the Orkneys were still connected with the mainland. And these again must have been isolated sufficiently long to enable the new species to become evolved from the ancestral type. Yet *Microtus agrestis* does not occur in the Forest Bed, nor does any other recent vole. All the Forest Bed vole remains have been shown by Dr. Forsyth Major to belong to extinct species and genera.

In this review of the Scottish fauna and of its north-western outliers, including Iceland, the most interesting feature, which has been clearly brought out, is that a land-connection formerly existed between Iceland and Scotland by way of the Faröes, Shetlands and Orkneys. Ample evidence has been adduced in support of this contention, but I think the occurrence of the field mouse in Iceland, of the orchid *Habenaria albida*, the snail *Arianta arbustorum*, of the Hemiptera, *Corixa carinata* and of *Orthezia cataphracta* on several areas intermediate between it and the mainland suggest that the land-connection might have existed certainly as far back as Pliocene times. These animals would consequently have survived the Glacial period on the lands occupied by them now. Whether Scotland was connected with Scandinavia as well will be discussed in another chapter.

CHAPTER IV.

THE general features of the English fauna have already been commented upon. The northern element, which forms so conspicuous a character in Scotland, is still represented in England, but the animals belonging to it become rarer as we go southward.

Take, for example, our British grouse (*Lagopus scoticus*). It is peculiar to the British Islands, but it is only the southern representative of the willow grouse (*Lagopus albus*) of Northern Europe. Whether our grouse is the descendant of the willow grouse, as has been maintained, or whether both have sprung from the same stock independently, are questions which need not concern us at present. There can be no doubt that the two species are extremely closely allied, and our British grouse must be looked upon as a northern bird. It is principally found in Scotland and Ireland, while in England it occurs as far south as Shropshire.

I might mention that the little white flowering orchid (*Habenaria albida*), which I cited in the last chapter as occurring as far west as Iceland and which is a typically Arctic and Alpine species, ranges even as far south as Sussex.

There is no need to dwell any longer on the presence in England of this Arctic element. It is met with, of course, principally in the northern counties and in Wales.

We possess in England, chiefly confined to the south-western counties, another faunal element which is particularly characteristic of Ireland. This English Lusitanian fauna agrees in so many respects with the Irish that there seems little doubt that both belong to the same group which travelled northward from South-western Europe at a comparatively remote period in the history of the British Islands.

Some of these south-western species penetrated along the

ancient west European coast-line as far north as Devonshire and Cornwall; others went still further north to Ireland, and many of the latter species subsequently became extinct in the intermediate tract of their former range. *Geomalacus maculosus* and *Trichoniscus vividus*, and, among plants, *Arbutus unedo* and *Saxifraga umbrosa*, as we have noticed, belong to the latter category.

Among such species which still occur in widely separated areas, both in England and Ireland, I might mention the small ant *Stenammina Westwoodi*. It has been found in the south-west of Ireland and in the south of England; nowhere else in the British Islands. Abroad it is confined chiefly to Southern and Central Europe. One other species of this genus inhabits the south of Europe and North Africa. Still another lives in California.

The spider *Teutana grossa*, a conspicuous object, has a very similar range in the British Islands. Abroad it is a characteristically Mediterranean form extending from Greece to the Canary Islands and the Azores.

The typically Lusitanian snail *Hygromia revelata* is quite limited to Devonshire and Cornwall, as far as the British Islands are concerned. It has likewise been met with in the Channel Islands, in Belgium, Western France, the Spanish peninsula, and in North-western Africa.

There is a group of molluscs which differ from slugs externally in so far as they have attached to their tail a small flat shell. Their subterranean habit places them in the foremost rank among those species which are of importance in tracing former changes of land and water. One of these (*Testacella maugeri*) (Fig. 23) is known from the south-west of England and the south of Ireland. Abroad it inhabits chiefly the south-west of Europe.

There exists in the south-west of England a centipede (*Lithobius pilicornis*) about an inch in length, which abroad so far is only known from Marocco, Madeira, and the Azores. The dragon fly *Oxygastra Curtisii* has been taken in the same district in England. On the Continent it occurs in the Spanish peninsula and in South-western France.



FIG. 23.—*TESTACELLA MAUGEI*, WITH ITS GEOGRAPHICAL DISTRIBUTION IN THE BRITISH ISLES.

Finally I might allude to two rather conspicuous plants belonging to the same Lusitanian group. The Irish spurge (*Euphorbia hiberna*), as it is called, grows in great profusion in many parts of Southern and Western Ireland. In England, on the other hand, it is a great rarity, and is evidently on the verge of extinction, being only found in a few localities in Devonshire. On the Continent it reappears again in Western and Central France and in the Pyrenees. The next species, known as the Cornish heath (*Erica vagans*), is absent from Ireland. It grows all round the Mediterranean and along the west coast of France. On our side of the Channel it is only known from Cornwall.

Very rare in England are the species of North American origin, such as the pearl mussel (*Margaritana margaritifera*) (Fig. 9). Its range in England is very instructive, for it is quite absent from the whole of South-eastern England, the area so characteristic of the Germanic species.

I have on several occasions referred to these Germanic forms and we must now examine them a little more in detail.

In his classic memoir on the origin of the British fauna Prof. Forbes informs us that the great mass of the British plants, every quadruped not found in Scotland or Ireland, and many of our land and fresh-water molluscs migrated to the British Islands across a land surface from the Germanic regions of the Continent. Forbes, therefore, limited the term "Germanic" to such quadrupeds or mammals which did not cross the boundaries of England. It is manifest, however, that, even among those mammals which have been able to penetrate into Scotland, many have advanced with this eastern or Germanic invasion of our area. I have explained that, especially among mammals and reptiles, a good many species are met with in Scotland which belong to the Germanic element. The dormouse (*Muscardinus avellanarius*) is one of those forms which have not been able to spread far north and which have more or less preserved the characteristic range of the Germanic species in England. Its Continental range, and the fact that no member of the genus to which it belongs has as yet been found, either

recent or fossil, outside the limits of Europe, suggests that the dormice and their allied genera all originated on our Continent.

The sand-lizard (*Lacerta agilis*) has only a very local range in England. Abroad it frequents Central, Northern, and Eastern Europe as well as Western Asia.

Four of our well-known fresh-water fishes are confined to Great Britain in the British Islands. They are the barbel (*Barbus vulgaris*), the roach (*Leuciscus rutilus*), the chub (*Leuciscus cephalus*), and the dace (*Leuciscus vulgaris*). The roach and chub are known from Scotland, but the barbel and dace are only met with in England. On the Continent, the four species are found throughout the greater part of the plain of Europe. They have most probably come from the east.

Among the invertebrates and plants, a very large percentage of the English species are more or less confined to the south-eastern counties. The continental range of such species points to their having entered British territory from the east, and that is why we group them among the eastern or Germanic forms.

The largest beetle in the British Islands, the so-called stag beetle (*Lucanus cervus*), is not one easily overlooked by naturalists. Its geographical distribution in our area is therefore of particular importance. It has been taken almost throughout the south of England. Towards the Midlands it becomes very rare, Derbyshire being the most northern county in which it has been observed. It inhabits the greater part of continental Europe.

Another large British insect, the swallow-tail butterfly (*Papilio machaon*), is still to be found in the fen districts of Norfolk and Cambridgeshire, and in Sussex, Essex, Kent, and Somerset, though it is becoming scarce. It is a common butterfly on the Continent, and is distributed almost throughout Europe and Asia.

Typically Germanic are the two fresh-water mussels *Unio pictorum* and *U. tumidus*. They are quite confined to England and Wales, and neither reaches Scotland or Ireland. On the Continent they occur throughout the European plain except in the extreme west.

There are numbers of land molluscs belonging to this Germanic group. Two of our Clausilias (*Clausilia biplicata* and



FIG. 24.—THE ROMAN SNAIL (*Helix pomatia*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

Clausilia Rolphi) scarcely penetrate as far north as the Midlands. They have a markedly eastern range on the Continent. Among the most conspicuous molluscs appertaining to this Germanic element is the Roman snail (*Helix pomatia*) (Fig. 24), so

called because it was formerly believed to have been introduced to this country by the Romans as an article of food. To this day it is held in high esteem on the Continent as a nutritious dish. Since it has now been discovered in pre-Roman deposits, we must assume it to have crept to this country unaided by man. It is limited in its range to the south-east of England, while its continental distribution indicates that it originated probably somewhere in the south-east of Europe, where, moreover, most of its nearest relatives live at the present day (*cf.* p. 199).

The examples of mammals, reptiles, fishes, insects, and molluscs I have quoted as inhabiting chiefly the south-east of England reveal to us clearly by their continental range how they have gradually pushed their way westward from the east. We are justified, therefore, in employing for them the term eastern or Germanic in a wide sense. This conviction that the south-eastern part of our area is largely inhabited by eastern species becomes greatly strengthened when we examine the remains of the many animals which have been brought to light in the superficial strata of the same district.

In our caverns which contain deposits belonging probably to a great extent to the Pleistocene—the most recent geological period—and also in the brick-earths, we find a most interesting assemblage of animal remains. Among the most remarkable of these are several kinds of small rodents, such as picas (*Lagomys*) and susliks (*Spermophilus*), together with an ungulate animal the size of a goat, known as the saiga antelope (*Saiga tatarica*). These now inhabit the steppe-like districts of Eastern Europe and Asia. None of their remains have been unearthed in the Spanish peninsula or in Italy, while in France and Germany their bones have been traced in recent deposits similar to those in our country. We thus obtain a perfectly conclusive history of an invasion of our area in recent geological times from the east, when undoubtedly England formed part of continental Europe. There are other rodents, the hamster (*Cricetus frumentarius*) (Fig. 25), for instance, which did not advance so far as England, though its remains have been discovered in France.



FIG. 25.—THE HAMSTER (*Cricetus frumentarius*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN EUROPE.

After having pushed into France, it then apparently retired as far as Eastern Europe. In more recent times it is again gradually forcing its way westward.

Among these English mammalian remains there is also an Arctic group, of which the glutton, musk ox, and reindeer probably formed part, which descended from the north.

Still another group, to which belongs the lion (*Felis leo*) (Fig. 54), can be traced to a south-eastern origin.

The lion is supposed to have lived in South-eastern Europe within historic times. It certainly hunted game in Middle and Western Europe at the time when the eastern steppe animals, just referred to, arrived in England, and it followed them and many larger ones which swarmed into our area. That the lion inhabited this country within such recent times may seem surprising, but it is by no means such a delicate animal as is generally assumed. Allusion has already been made to the fact that in the Dublin Zoological Gardens a pair of lions have been kept in the open, night and day for the past four years. They have not only stood the winters remarkably well, they have even reared their young under these conditions.

Of even greater importance than the lion, from a distributional point of view, is the occurrence in England as far north as Yorkshire of the remains of the hippopotamus (*Hippopotamus amphibius*) (Fig. 26). Its bones have been discovered in the same deposits as those of the lion. Certainly the fact that this unwieldy creature, which is so much bound to a semi-aquatic life in lakes and rivers, should have found its way right across Europe to England, is of the utmost importance. From our knowledge of the habits of this animal, it is difficult to conceive how it could have lived in this country unless the climate was mild enough to keep the rivers entirely free from ice during winter. The hippopotamus, then, appears to be a safe guide in obtaining an estimate of the nature of the climate in Northern Europe at the time when these south-eastern animals entered England. For Professor Boyd Dawkins's attempt to explain the mingling of the African forms of life with those from the Arctic regions and the East by the supposition that there was an enormous seasonal

variation of the climate, so that the hippopotamus could migrate southward in winter and back again in the summer, does not



FIG. 26.—THE HIPPOPOTAMUS (*Hippopotamus amphibius*), WITH ITS PAST RANGE IN EUROPE AND NORTH AFRICA MARKED IN BLACK.

harmonise with our modern experience of the habits of that species.

It is evident that the great majority of the British mammals

that have been alluded to hitherto, have travelled very far from their original homes and have traversed many countries before finally reaching the British Islands. Some of them may have originated in Asia, others in Africa or even America. The insects, and the slowly moving molluscs especially, can mostly be traced to a European origin. In this way many species, say, for example, of an Alpine origin, may have entered our area together with such that started their travels from Africa or Asia.

There are some European molluscs which appear to have had their original home beyond the confines of our Continent, such as *Eulota fruticum* (Fig. 27). Its ancient home must be looked for in Asia, because all the remaining members of the genus to which it belongs are Asiatic. Moreover, if it were a native of Europe, we might expect it to have ascended the upper regions of the Alps, since it occurs in Northern Russia and Scandinavia. But it did not do so. It already reached England in pre-Glacial times. It has also been noticed in several English Pleistocene deposits. To judge from this evidence, we must presume that it remained in this country for a considerable time, and only became extinct with us quite recently. In the European plain it is still a common species as far west as Northern Spain. Reference will be made to it again (p. 164) later on.

Patula ruderata, an Arctic-Alpine snail, has only been noticed in this country in English Pleistocene deposits. Evidently a late immigrant, it has soon died out again. In the European plain it still exists in a few isolated localities. It is only common in Siberia, Scandinavia and in the higher Alps.

These few examples will give an idea of the evidence we possess from fossils as to the arrival in England of an eastern fauna.

We have, however, evidence, too, of Lusitanian species, now no longer living in this country, having become extinct in recent times. The Rev. Ashington Bullen discovered close to an early cemetery, at Harlyn Bay, in the grave level of the soil, the shell of a snail which is only found living at the present



FIG. 27.—*EULOटा FRUTICUM*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

day in Spain and Portugal. This species, *Hygromia montivaga*, is probably only one of a group of south-west European molluscs which have gradually become extinct, within recent times, in their more northern habitats.

I have now given a general survey of the various elements constituting our fauna and have attempted to trace some of the individual members to their original native lands. But, besides the species which can be readily classified into one or the other group of animals, there are some, for example, the pond snails, *Limnæa perèger* and *L. palustris*, which are found practically everywhere in the British Isles. On the Continent, too, wherever we examine any lake or pool, we are almost sure to meet with them. Even when we cross over to North Africa or into Asia, they are still common. One of them, *Limnæa palustris*, occurs likewise throughout Siberia and in part of North America. They are evidently species of great antiquity. Owing to their extreme adaptability to changes of climate, they have been able to maintain themselves in those parts of the world which they invaded. It is not readily ascertainable, in the present state of our knowledge, in what part of the world they have originated, and how they came to be in our islands, or, rather, what particular element in our fauna they belong to.

It must not be thought that the whole of our fauna has come to us from continental Europe or America. Dr. Wallace has pointed out in his "Island Life" that there are quite a number of forms of animal and plant life in these islands which have not yet been found elsewhere, and which we might presume to have originated in our area. Our grouse, for example, though so closely allied to the Scandinavian willow grouse, is looked upon as a distinct species. I have also had occasion to refer to our two indigenous voles. Several of our fishes, such as the pollan, vendace and gwyniad, though very nearly related to Scandinavian forms, are likewise regarded by many ichthyologists as good species. There are, moreover, a number of insects which have not yet been recorded beyond the seas that separate us from the Continent. Then we possess a few peculiar snails,

such as *Limnæa involuta* and *Pisidium hibernicum*, both confined to Ireland, and some plants especially among the cryptogams.

There are a few others which, though they have probably their ancient home in this country (as for example the delicate silken-textured snail, *Acanthinula lamellata*), have spread in the course of time to other countries. *Acanthinula lamellata* is found sparingly in Sweden, Denmark and Northern Germany. It may have radiated out to these countries from its British centre.

But when we come to add together all these species, which we may reasonably suppose to have had their origin in our islands, they constitute really a very insignificant number as compared with the great mass of those that have reached us from abroad. The number is in fact so small that we scarcely need to discuss their relationship. It is significant to remember, though, that of those indigenous species whose relations we are acquainted with the great majority live either in the North or South. It is a confirmation of the theory first advocated by Forbes that the southern and northern elements of our fauna are much older and would have had more time to develop new species than the eastern element.

We have now come to a stage in our enquiries into the geological history of our fauna when we should take a survey of all the general facts of distribution with which we have become acquainted. I have roughly indicated the bearings of these facts on the very important questions of the age and history of our animals. It only remains for me to collate the various threads in order to present a more uniform picture of the events in the history of our fauna.

The distributional facts which I explained indicate that our fauna, as well as our flora, are obviously composed of a number of elements or groups. Leaving out the indigenous group of animals and plants, which is insignificant, we can trace a small group which reached us from North America by means of an old land connection. This land bridge stretched right across the Northern Atlantic Ocean to Europe. There is a much larger group of northern and Alpine animals and plants. Part of it

certainly invaded England from Scandinavia, while another appears to be derived from the Western Alps.

A South-west European, or Lusitanian, group of animals and plants travelled to our area from the Spanish Peninsula, at a time when our islands were raised so much above sea-level that a continuous shore-line extended between Ireland and Brittany and between Ireland and Scotland. The Irish Sea was then dry land, except for a large fresh water lake in the middle of St. George's Channel (Fig. 13). Finally an eastern, or Germanic, group invaded these islands, whose origin may be either in Central or Eastern Europe, or even in Asia or Africa. This large Germanic group can again be subdivided on that account into a northern and a southern branch.

Edward Forbes believed that the Lusitanian element in England was the oldest, and I think there can be no doubt about its being so. The American element may be almost of equal age. But it is quite evident, that both of them poured into this country during a long series of centuries. Some of the Lusitanian species appear from their general range to be much more ancient than others, implying that a gradual northward movement of animals and plants continued, perhaps, through several geological periods. Towards the close of that northward advance, the American group probably entered our area. All this took place when our islands were at a high level. The land sank then, or the sea rose, whichever view we like to take does not matter for our purpose. The chief factor was the altered geographical conditions of our islands. They now slowly assumed their present shape. Scotland was still connected with Northern Ireland and with Scandinavia when the Alpine and northern species entered our territory. Now at last the Germanic wanderers began to make their appearance on our shores, first the more southern forms and finally the eastern steppe animals and plants. A narrow land bridge then still connected England with France. Ireland now assumed its independent existence, which, I think, it has preserved ever

since. In this manner it was brought about that the Siberian fauna is so conspicuously absent from our sister isle.

Taking into consideration the testimony yielded by the remains contained in the recent English Tertiary and post-Tertiary deposits, I am of opinion that the whole of the existing Irish fauna and flora is of pre-Glacial Age. That is to say, it must have arrived in Ireland before Pleistocene times, and a remnant of it persisted there until the present day. The Siberian section of the Germanic group in Great Britain is of Pleistocene Age. The representatives of the older elements in England and Wales have been driven into isolated corners by the more vigorous new-comers from the East, and many are rapidly becoming extinct. In Ireland, on the contrary, the Arctic hare thrives throughout the country down to sea-level, although the climate is milder than that of Great Britain. By the advent of the continental hare in Great Britain the Arctic hare has been compelled to take refuge in the mountain recesses of Scotland. Similarly, the mountain avens (*Dryas octopetala*), one of our most typically Arctic plants, has been preserved to us on the west coast of Ireland, where it grows in close vicinity to the delicate Lusitanian plants, so characteristic of the Irish flora.

Palæontologists have vainly attempted to unravel the causes of the apparently anomalous mixture of southern and northern types of animals in our Pleistocene deposits. But is this mingling really so exceptional? Do we not perceive something of that nature in almost all European countries at the present day, but especially so in Ireland?

From these remarks it must be evident that I do not believe in the exceptional destruction of our fauna and flora during the Glacial period. There can be no doubt that many species did become extinct, but we notice precisely the same feature in passing from any one geological formation to the next. Even within historic times we know that species have died out, quite independently of man's influence over them. It seems to be a law of nature that some kinds of animals and plants are destined to survive scores of others which come

and go, often leaving scarcely a trace of their fleeting existence.

I cannot here essay to describe the various phases of the Glacial period or its cause. That has been done very fully by others. There is only one point which should be remembered, and that is that there is no period in all geological history on which there exists a greater diversity of opinion. Even on the subject of the climate during the Glacial period some geologists hold diametrically opposite views to others. For, whilst the majority urge that the temperature was much lower than what it is now, others maintain that it must have been higher.

It is generally conceded that there was at least one mild interlude called "inter-Glacial period" separating two phases of cold climate. But it is also maintained by some that there must have been two, three, or more of such mild phases, while the existence of any inter-Glacial stage has recently been denied by Mr. Lamplugh in his presidential address to the geological section of the British Association.

While I follow Edward Forbes in his main contentions regarding the origin of our fauna and flora, I do not agree with his views as regards the Glacial period. No one, I think, can believe in the survival of a southern group of animals and plants in the British Islands through the Glacial period, without at the same time admitting that the climate was mild throughout. That glaciers existed more extensively than at present cannot be denied. A more uniformly humid climate in Europe may have favoured the production of glaciers without decreasing the temperature.

Professor Carpenter and Dr. Stejneger agree with Professor Forbes and myself in admitting a survival of the Lusitanian fauna and flora through the Glacial period, while Mr. Bulman contends that the climate was such as to permit the existence of temperate life not only in the south of England, but in other favoured localities in the British Islands.

Before concluding this chapter, a few remarks might not be out of place on the evidence which the marine fauna

furnishes us as to the existence of a former continuous shore-line between Brittany on the north-west coast of France and Ireland. In his work on the "Building of the British Isles," Mr. Jukes-Browne publishes an interesting map of our islands as he believes them to have presented themselves in newer Pliocene times, that is to say, just before the advent of the Glacial period. A continuous coast-line then extended between Western France and Ireland. The waters of a mighty river rolled down the English Channel, while another flowed down the St. George's Channel. More recently Professor Hull has taken up the study of an investigation of the sub-oceanic region adjoining the British Isles, with the aid of the Admiralty charts of soundings. Similar investigations made on the American coast of the North Atlantic by Professor Spencer had revealed the remarkable fact that ancient river valleys can be traced far away from the coast—a clear proof that the land formerly stood at a higher level than it does now. So, also, on our coast Professor Hull was able to trace ancient submerged river channels, formed at a time when the platform on which our islands rest was raised considerably above the level of the sea.

From purely distributional facts, we arrive at precisely similar conclusions. Most of our shore forms of animal life travel along the coast, advancing from one country to another, much as land animals do—not by leaps and bounds, but slowly, step by step. Very frequently their eggs are carefully attached to fixed objects, so as to prevent their being carried away by the action of the waves, whilst the young often remain and grow old in some particular little pool.

Quite a number of such coast species occur on the west coast of France and on the south-west coasts of England and Ireland. Their present discontinuous range was manifestly continuous at the time of the existence of the old coast just referred to.

A very familiar example to British zoologists is the rock-boring purple sea-urchin (*Strongylocentrotus lividus*). *Inachus leptochirus*, *Gonoplax angulata*, *Thia assidua*, and *Callianassa subterranea* are crustaceans with a similar range. The fishes

Blennius galerita and *Lepadogaster Decandollii* and the mollusc *Otina otis* likewise belong to the same category.

There are, moreover, a few semi-marine species—creatures which live close to high-water mark, such as the insects *Octhebius Lejolisi* and *Aëpophilus Bonnairei*, whose geographical distribution in the British Islands corresponds with those just mentioned.

Thus, the occurrence of these species on the Irish coast, in the south-west of England, and on the west coast of France greatly strengthens the evidence that these three disconnected areas were joined within comparatively recent geological times.

CHAPTER V.

IN the last three chapters I have dealt with the geological history of the animals of the British Islands in detail, because, as I have had occasion to mention before, the fauna of these islands contains the key to the solution of the wider problems embodied in the geological history of the European fauna as a whole. I have felt that a careful study of the questions at issue, as regards our own islands, would enable us to better appreciate similar enquiries in other countries.

In the course of my observations on our fauna and flora, I have rendered an account of a stream or wave of dispersal, which I supposed to have issued from South-western Europe, and to have wandered to our area during Tertiary times. The reason for such a supposition was that most members of our Lusitanian element had their headquarters in that part of Europe. They could only have travelled northward at a time when the climate of Europe was more favourable to their extension than it is at present. I presumed they were representatives of a very ancient dispersal, because almost all the members of that South-western, or Lusitanian, element in our fauna have a discontinuous range, which is a sure indication of great antiquity.

I propose in this chapter to proceed to the home of the Lusitanian fauna—to the Spanish Peninsula—in order to ascertain what light the animals and plants of that country may throw on the geological history of the European fauna as a whole.

The name "Lusitania" was first used by the Romans when, under the Emperor Augustus, the Spanish Peninsula was divided into three provinces, one of which, "Lusitania," coincided with a large portion of the present area of Portugal. The term "Lusitanian" is, therefore, almost synonymous with

Portuguese, though it is frequently applied by zoologists and botanists in a much wider sense, so as to vaguely include the extreme south-west of Europe without any definite limits.

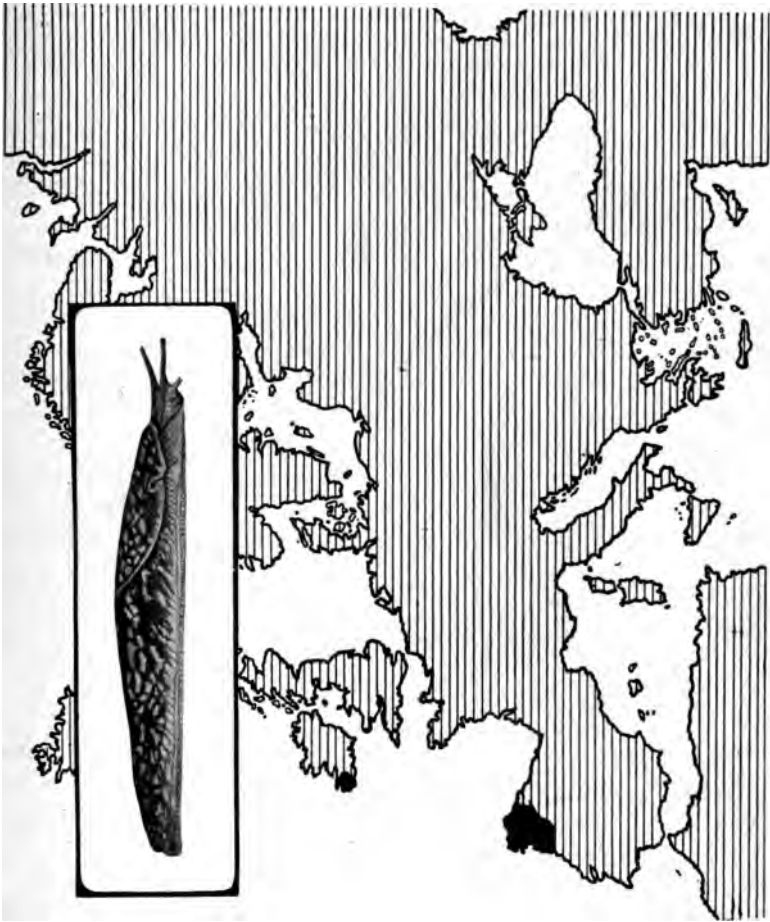


FIG. 28.—THE SPOTTED SLUG (*Geomalacus maculosus*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

One of the most typical members of our Lusitanian fauna is the spotted slug, *Geomalacus maculosus* (Fig. 28). It was first discovered in Ireland, and it has since been met with in Northern Portugal. Two other species of this remarkable

genus *Geomalacus* have been found in Portugal, viz., *G. anguiformis* in the central provinces, and *G. Olivieræ* in the south. The genus *Geomalacus* is related to the North-west African *Letourneuxia*, which has sent an off-shoot to Gibraltar. The fauna of the latter place is, as we shall learn later on (p. 98), intimately allied to that on the south side of the strait. *Letourneuxia numidica* is only known from Gibraltar on our Continent, whilst in North Africa it ranges from Algeria to Marocco. Both *Geomalacus* and *Letourneuxia* belong to the family Arionidæ, to which, also, many of our common slugs belong. Professor Simroth urged that the cradle of this family of slugs probably lay in South-western Europe. From this centre of origin the genus *Arion* (Fig. 29) has radiated north, east, and south, so that at the present moment we find five species in the British Islands and the same number in Germany. Further north, and also further east, the number of species diminish. Four crossed the Russian frontier, but only a single one penetrated beyond, and even became so modified as to form a distinct species in Siberia. We have here a Lusitanian genus, which has been able to adapt itself, apparently with ease, to extremely low temperatures, and is still pushing its way eastward. Dr. Pilsbry locates the origin of the family in America, and contends that it has spread from there across the Bering Strait to Siberia and Europe. That the American forms present more primitive types seems probable. But, to judge from the general distribution, it is more likely that the ancestors of *Arion* crossed the Atlantic to Europe in early Tertiary times than that they used the circuitous route suggested by Dr. Pilsbry.

Before proceeding with the detailed study of the Lusitanian area, I might refer to some endeavours that have been made to distinguish its faunistic elements.

About ten years ago two important contributions appeared, one by Dr. Gadow, dealing almost exclusively with the Spanish vertebrates, and the other by Dr. Kobelt, describing the chief characters of its molluscan fauna. Both authors came to the conclusion that the Spanish Peninsula must be divided into two distinct provinces—a northern and a southern. But whereas

Dr. Gadow's boundary is formed by the high mountain ranges which extend from Cape Finisterre to Castellon, Dr. Kobelt



FIG. 29.—MAP OF EUROPE AND ASIA, INDICATING THE GEOGRAPHICAL DISTRIBUTION OF THE SLUGS BELONGING TO THE GENUS *ARION*.

places his division of the Spanish Peninsula much further south. It corresponds more or less with a broad zone of Tertiary rocks, extending from the Mediterranean coast to the Atlantic at a point where these two seas communicated in Miocene times.

Dr. Gadow recognises in his southern province a distinct African element, while Dr. Kobelt goes so far as to dissociate his corresponding Andalusian province from Europe altogether. In Southern Spain, he remarks, we are conchologically on African soil.

The flora of Spain has recently been very thoroughly investigated by Prof. Willkomm. He divided the Spanish Peninsula into six districts, each of which has its peculiar plants. The whole flora, according to him, is composed principally of endemic Central European, and also of Mediterranean, North African, and Atlantic species. A considerable number of plants are common to the Spanish Peninsula and North Africa.

It is difficult to say which part of the Spanish Peninsula is faunistically the most interesting; but the Pyrenees, in many respects, offer the greatest attraction to the naturalist. That the Pyrenees have always acted as an obstacle to the dispersal of species from the East to the West, or *vice versâ*, must be evident. I showed, however, some years ago, that many widely-spread forms have succeeded in crossing the mountains, while to the north and south of them there is a level coast region, where an extensive interchange of the fauna is taking place, and has done so in the past, between France and Spain. Yet the Pyrenees constitute the boundary of their western range for many species, such as *Arianta arbustorum* (Fig. 21), and also for the eastern voles, which, as we have learnt, are absent from Ireland.

The Pyrenees are noteworthy from the fact of their possessing several endemic species which have their nearest relatives in Eastern Europe.

The Pyrenean musk rat (*Myogale pyrenaica*) inhabits, apart from the Pyrenees, the mountainous regions of Northern Spain and Portugal. It is closely allied to the mole, and therefore not a rodent, but a true insectivore. Like the otter, it spends the greater part of its existence in the water, and only quits it during resting hours and when tending its young in the subterranean burrows close to the water's edge.

We have to travel right across Europe to the steppes of

Southern Russia to again meet with a musk rat—a near relative of the Pyrenean form, called *Myogale moschata*.

The musk rat seems to have originated in Europe. We possess fossil evidence of the occurrence of the eastern musk rat from Germany, Belgium, and the Forest bed of England. In earlier times, the ancestral form of our two musk rats must have had a wide range in Middle and Northern Europe, probably at a time when that part of our continent was completely separated from the south by a wide ocean. At that period certainly three species inhabited France. The present discontinuous range of the genus *Myogale*, being confined to the two corners of Europe, points to its being an ancient survival of late Tertiary times, when the geographical features of our continent differed greatly from what they are at present.

Another mammal, belonging to the same category as the musk rat, is the Spanish wild goat (*Capra pyrenaica*). It lives high up in the Pyrenean mountains, and though now extinct in the Cantabrian range, which skirts the northern coast of Spain, it occurred there formerly. We meet with it again in Northern Portugal, and with an allied species in the mountains of Southern Spain. Its former wider range over the Spanish Peninsula is proved by the occurrence of its remains in the caves of Gibraltar. We should expect this wild goat to resemble the Alpine ibex or "Steinbock," but it is much more closely related to the wild goat of the Caucasus (*Capra cylindricornis*).

A still more striking instance of discontinuous distribution is known among birds, for the beautiful blue magpie of Spain (*Cyanopica Cooki*) has its nearest relation (*Cyanopica cyana*) in China and Japan. The two are scarcely distinguishable, while no member of the genus is found in the intermediate tract.

As I shall show later on (p. 129), the Alpine area was for a long period in later Tertiary times connected directly with Central Asia. We may suppose that many Asiatic forms entered Europe by means of this land connection, from which they subsequently spread into the plain, when the seas then surrounding the Alps, in the north and west, retreated. Climatic conditions in the

Alps then changed, with the result that many species were probably exterminated there which were able to persist in the plain. The distribution of the blue magpie of Spain might be explained in such a manner, though it very possibly has found its way to Europe along the southern margin of the ancient Mediterranean by way of Northern Africa.

However, to return again to the Pyrenees, besides the eastern forms, these mountains have a large number of species in common with the Alps. Noteworthy instances are the chamois (*Rupicapra tragus*) (Fig. 44), found westward as far as the western limits of the Cantabrian mountains in Spain, and the marmot (*Arctomys marmotta*) (Fig. 45), which probably still exists in the same region. It is not certain whether fossil remains of the Alpine marmot occur in the European plain. In several localities in Germany, where marmot remains were met with in Pleistocene deposits, they were identified as the eastern marmot (*Arctomys bobac*), closely allied to the Alpine form. Marmot remains have been discovered in Siberia, Russia, Austria, Germany, Belgium, and France, in Pleistocene deposits.

The entomologist who explores the Pyrenees in quest of peculiar butterflies will find many endemic kinds, but likewise such as the handsome and stately Apollo (*Parnassius apollo*) (Fig. 43), so typical of Switzerland. And similarly the botanist will encounter the Alpine rhododendron (*Rhododendron ferrugineum*) and the edelweiss (*Leontopodium alpinum*), with which he has been familiar as Alpine species. A few of this group of Alpine forms, which have spread to the Pyrenees, have even penetrated to the Sierra Nevada.

Still other Pyrenean forms of life exhibit relationship with Sardinia and Corsica. The brightly coloured Pyrenean newt (*Molge aspera*), which may be found in the streams above the famous baths of Eaux Chaudes, has its nearest kin in the islands just referred to. We have to go back as far as very early Tertiary times, to the Miocene or perhaps Oligocene period, to explain the origin of this relationship. It was then that part of the present Pyrenees was still submerged in the sea which formed a wide gulf eastward from the Bay of Biscay. The

older portions of the mountains were probably joined to Corsica and Sardinia in one continuous land mass. This land was then separated from the Alps, which began slowly to rise as an island in the midst of the Tertiary seas.

Finally, at the foot of the Western Pyrenees, there are a few relics of past ages which may have persisted on islands when the surrounding areas were submerged. Only four species of the mollusc *Clausilia* have reached the Pyrenees from the



FIG. 30.—CLAUSILIA PAULI (TWICE NATURAL SIZE).

east. But, besides these, there occurs in one isolated locality near Biarritz, in Southern France, a *Clausilia*—the only European survivor of the sub-genus *Laminifera*. This species, *Clausilia Pauli* (Fig. 30), is akin to a number of forms found in German and Bohemian Oligocene and Miocene deposits. Its nearest living relatives all inhabit South America. Near the same district, and all along the foot of the Cantabrian mountains as well as in a single locality in Brittany, another mollusc has been discovered which occupies a still more isolated position

among European land shells than *Clausilia Pauli*. Resembling the fresh-water genus *Planorbis* in external appearance, this peculiar species of terrestrial mollusc, known as *Elona quimperiana* (Fig. 31), is probably a survival on lands which have remained unsubmerged for long ages past.

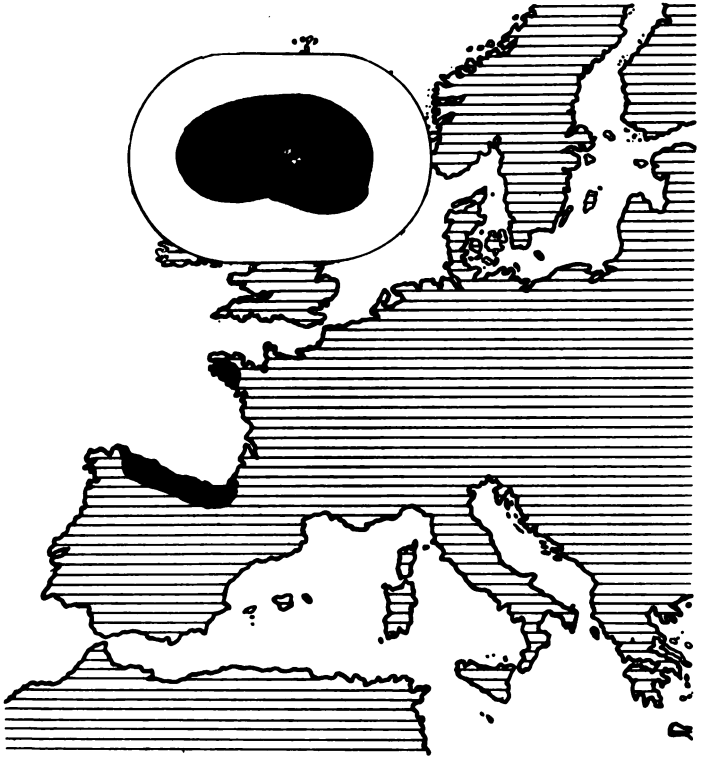


FIG. 31.—*ELONA QUIMPERIANA*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

The peculiarly Alpine terrestrial molluscs of the genus *Campylæa* are completely wanting in the Pyrenees. Of the Lusitanian genus *Gonostoma*, which in Central Europe is represented by only three species, five peculiar forms occur in the Spanish Peninsula, including the Pyrenees. None of the latter

have spread northward, but the Central European *Gonostoma obvoluta* has penetrated as far north as Northern Germany and Southern England at a time when the latter was still connected with the Continent.

As regards the faunal elements of the Spanish peninsula, the mammals which were able to reach Ireland are almost all known from Spain too. Several which have become extinct in the former country within recent times, such as the bear (*Ursus arctos*), the wolf (*Canis lupus*), and the wild boar (*Sus scrofa*), still exist in Spain. All the common Irish mammals, the otter, marten, badger, hedgehog, fox, rabbit, and others, inhabit Spain; and there are some additional ones in the country unrepresented in Ireland, of which we have reasons to believe that they came from the east, for example the weasel, polecat, mole, and roeder.

Two Arctic mammals are known to have wandered to Spain. One of them, the Arctic hare (*Lepus timidus*), still occurs in the Pyrenees, while the other, the Norwegian lemming (*Lemmus lemmus*), discovered by Dr. Gadow in a Portuguese cave, is now extinct in the Spanish peninsula. It is significant that both of these occur in Ireland, one living and the other extinct. It is quite possible that the reindeer may also have reached the peninsula, though no definite records are known. We have reasons to believe that many mammals entered Europe from the south-east. Of these some are extinct; most of them are still living. The mammoth, the hippopotamus, the spotted hyæna, probably all came with that group, and all penetrated into the Spanish peninsula.

Of the existence of a distinctly southern mammalian fauna in Spain we have evidence from the Gibraltar cave remains, while, apart from the rock ape (*Inuus ecaudatus*), which may possibly be introduced, the genet (*Viverra genetta*) and the Spanish ichneumon (*Herpestes Widdringtoni*) deserve special mention. The latter is a form of the African ichneumon (*Herpestes ichneumon*).

Among the reptiles, the Moorish gecko (*Tarentola mauritanica*) (Fig. 32), the Algerian sand lizard (*Psammodromus algirus*), the grey

amphisbæna (*Blanus cinereus*), which leads a subterranean life, the Spanish terrapin (*Clemmys leprosa*), a fresh-water tortoise, and many others occur in the Spanish peninsula and also on the opposite side of the Strait of Gibraltar. The painted frog (*Discoglossus pictus*), found on the west coast of the Spanish



FIG. 32.—THE MOORISH GECKO (*Tarentola mauritanica*).
PHOTOGRAPHED FROM A SPECIMEN IN THE BRITISH
MUSEUM (*Nat. Hist.*).

peninsula, likewise reappears in Marocco. Among the invertebrates, there are so many similar cases of distribution, that it would fill many pages to enumerate them. Some of them I shall refer to when we come to deal with the Western Mediterranean region.

The influence of the Strait of Gibraltar, as far as the land shells are concerned, is scarcely felt, so close is the relationship

between the fauna of Marocco and that of Southern Spain. We observe very similar features, perhaps not quite so strongly marked, among the beetles, the grasshoppers and their allies, and the centipedes and wood lice.

The Balearic Islands have many species in common with the Spanish mainland, and seem to have been connected with it, certainly in Pliocene times. No less than twenty-eight species



FIG. 33.—*TUDORA FERRUGINEA* (THREE TIMES NATURAL SIZE).

of land molluscs are peculiar to the islands. These are mostly related to Andalusian forms. One of the endemic snails, evidently a relict of early tertiary times, is of particular interest, viz., *Tudora ferruginea* (Fig. 33). Its only living relations inhabit the West Indies. On the mainland of Europe the genus is known from Miocene deposits.

Not only on the Balearic Islands, on the Spanish mainland too, we find a very large endemic element in the fauna. I have

mentioned the Spanish ichneumon and the blue magpie. Then there are two species of western voles (*Microtus lusitanicus* and *Microtus Mariæ*) belonging to the sub-genus *Pitymys* and the recently described large vole *Microtus Cabreraæ*. A lizard (*Lacerta Schreiberi*), a toad (*Alytes cisternasi*), a frog (*Rana iberica*), a newt (*Chioglossa lusitanica*), and very numerous invertebrates are all peculiar to the region. One of the most striking of the latter is *Iberus gualteriana*, from the south of Spain. Like *Elona quimperiana* (p. 96), it seems to be an ancient relict of past times. It has no near connections anywhere, and it has only been provisionally placed in the genus *Iberus*. The Spanish fauna is particularly rich in orthoptera, among which there are a large number of endemic forms.

I have now shown that the Spanish peninsula has been a centre for distribution of species, which have radiated eastward and northward, and we have learnt that this dispersal of species has been continued for long ages. I have demonstrated, too, that the area has been invaded by a northern fauna and by an eastern and a southern one, and, finally, that it contains a number of relicts from early Tertiary times.

I have reason to believe also that the Lusitanian fauna has spread westward to two groups of islands which are now far removed from the continent of Europe. These are Madeira and the Azores.

The history of these islands is in so far of great general interest as it is intimately connected with the ancient legend of Atlantis. The problem of the former existence of a great land beyond the pillars of Hercules has occupied human thought since the early dawn of history. Plato was the first to record the story of this mysterious land, to which the name of "Atlantis" was given. According to his narrative, Solon is said to have visited the city of Sais, in Egypt, and there to have heard from priests of the ancient empire of Atlantis and of its final overthrow by a convulsion of nature. From the account given by Plato, this Atlantis was a continent lying in the Atlantic Ocean beyond the Strait of Gibraltar.

Quite a flood of literature has appeared on this subject since

it was first handed down to us by Plato. By some it was scouted as a vague and inconsistent tradition. Others believed in the story, and republished the account with many fanciful amplifications of their own. Others again, in their zeal for speculation, enlarged the Atlantis so as to make it join the New World and the Old across the Atlantic, and argued that the early races of man must have wandered on this land bridge from Europe to America, and have peopled the latter continent in this manner.

Although the original narrative has thus led to some extravagant theories, thoughtful men have, from time to time, expressed their conviction either that it rests on some actual historic basis or that the legend was a vestige of a widely spread tradition. I need only mention in this connection the names of Humboldt and Sir Daniel Wilson.

The Atlantis problem, as we might call it, however, was only raised to scientific importance when modern research revealed the fact that the living, as well as the extinct, floras of Europe have quite a number of types in common with North America.

The first naturalist who attempted the solution of the Atlantis problem from a botanical point of view was Professor Unger, an Austrian botanist. The great Swiss naturalist, Professor Heer, elaborated Unger's theories, and argued that the prominent European character of the Atlantic islands, as shown by their plants and insects, proved that they were formerly connected by land with the continent of Europe. But, besides these forms, he noticed that certain American types occurred in all the islands, and that the flora of the latter, in some respects, resembled the Tertiary flora of Europe, which, again, was allied to that of America.

These remarkable features were explained by Heer by the supposition that, during the Tertiary era, the continents of Europe and America were joined across the Atlantic, and that the plants travelled on this old land connection from the one to the other. The plants of the Atlantic islands, he thought, were more European in character than American, because the

islands had been united with the Old World much longer than with the New.

Edward Forbes and Andrew Murray maintained that, at the close of the Miocene period, a vast continent extended far into the Atlantic from the coast of Portugal past the Azores.

In his presidential address to the Entomological Society of London, Dr. A. R. Wallace vigorously attacked Heer, Forbes, Murray, and others, contending that they had not grappled with the facts as a whole. He advanced evidence to show that the geographical distribution of the insects in Madeira, for example, is inconsistent with the theory of their dispersal to that island having been effected by a former land connection with Europe. Their transmission appeared to him to have been brought about by a passage through the air when assisted by gales and hurricanes. Hence Dr. Wallace does not believe that the fauna of Madeira and the Azores reached these islands by land from Europe.

It is not necessary here to repeat my arguments for upholding the older views against Dr. Wallace. I have published them in detail in a paper on the "Atlantis Problems," to which I would refer those who are interested in the subject. I should briefly mention, however, that Dr. Wallace founded his views upon the insects, and on three other important statements. He pointed out, in the first instance, that the Atlantic islands were entirely composed of volcanic rocks; secondly, that they were surrounded by great depths of water; and lastly, that they possessed no indigenous land mammalia.

As regards the first statement, that the Atlantic islands are composed of volcanic rocks, it does not necessarily imply that they could not therefore have formed part of the continent of Europe in former times, for even Professor Hartung, who made a special study of the geology of Madeira, looked upon the Atlantic islands as the summits of submerged mountain chains, while two other geologists, viz., Dr. Guppy and Professor Neumayr, maintained that these islands are the remnants of a great continent which united the Old World and the New.

Dr. Wallace's second statement, that the Atlantic islands

were surrounded by great depths, is only partially correct. On the map he published Dr. Wallace indicates a depth of 12,000 feet between Madeira and Europe; but it has since been demonstrated that there are shallow banks, only a couple of hundred feet below the surface of the sea, in that area. It is probable, therefore, that a narrow submarine ridge connects the island of Madeira with the coast of Portugal.

It now remains for me to deal with Dr. Wallace's third statement, that the Atlantic islands possess no indigenous land mammalia. He acknowledges that rabbits, weasels, rats, and mice are now found wild in the Azores, but believes these to have been introduced by human agency.

There seems to be no record, however, of any such introduction. We are led to assume that rabbits were brought over by the Portuguese when they first colonised the islands. But, when the discovery of the Azorean archipelago by a merchant sailing from Lisbon was announced in the year 1439, the most striking feature of the islands was the abundance of hawks or buzzards there. This circumstance induced the Portuguese to give the name of "Açores" (meaning hawks) to the islands. These hawks are still abundant on the islands, where they live chiefly on mice, rats, and young rabbits. Hence it would appear probable that small mammals already existed on the Azores when the Portuguese first set foot on them.

This supposition receives confirmation from a still earlier record of the history of the islands. It has now been ascertained that the existence of the Azores must have been known to early navigators even before the date just referred to. They were then evidently uninhabited by man.

The islands made their first appearance in print in an atlas of unknown authorship, probably drawn up by a Genoese, about the year 1345. A little later, in 1385, another atlas was published at Venice by Guglielmo Soleri, that is to say, more than fifty years before the discovery of the Azores by the Portuguese. The names of the different islands appearing on this atlas are of particular zoological interest, as they are evidently derived from the names of the animals which the early Genoese navigators

discovered on the islands. On Soleri's map of the Azores and of Madeira the names of the islands are indicated as follows:—

Capraria = Goat Island (now St. Michael);

Columbis = Pigeon Island (now Pico);

Li Conigi = Rabbit Island (now Flores);

Corvi Marini = Island of Sea Crows (? Shearwaters)
(now Corvo).

The result of these historical enquiries appears to justify the presumption that mammals, such as the goat and rabbit, are truly indigenous species on the Azores.

As regards the Azorean weasel, Captain Barrett-Hamilton has recently drawn attention to the fact that it belongs to a sub-species unknown from the European continent, though occurring also on an island off the west coast of Africa. That the weasel of the Azores was introduced there by the early discoverers seems extremely improbable. I am, therefore, of opinion, contrary to Dr. Wallace, that the existing mammalian fauna of the Azores supports the view that these islands were formerly connected by land with the mainland.

The fauna of Madeira and the Azores consists of European and North African immigrants and of an ancient endemic element of unknown origin. Among the latter the subterranean slug-like mollusc *Plutonia atlantica*, described by Professor Simroth, is especially noteworthy. Its presence alone speaks in favour of an ancient land connection with some larger terrestrial area.

As regards the period of origin of this endemic fauna, I should feel inclined to place it in early Tertiary and late Secondary times. The survival in the Azores of the molluscan genus *Craspedopoma*, which occurs on our Continent from Eocene to Pliocene deposits, and of the Madeiran *Janulus*, which is known from our Oligocene and lower Miocene beds, imply an early Tertiary colonisation of the islands.

The geological history of the Atlantic islands is intimately associated with that of Western Europe.

We know that the Pliocene period in Southern Europe was

ushered in by movements in the earth's crust which caused extensive subsidences between Spain and Marocco. The Strait of Gibraltar was thus formed between the Atlantic and the Mediterranean. The remarkable fauna of Northern Africa which is so characteristic of Southern Spain entered the latter region, therefore, at an earlier time, probably during the Miocene period. The greater part of the African molluscan fauna in Spain is to this day confined to the southern provinces, which in Miocene times were united with North Africa, and separated from the rest of Spain by a broad marine channel.

To recapitulate the results of our researches into the fauna of the Spanish peninsula, we have evidence of the existence of a very ancient endemic element. We have also seen that the Lusitanian fauna, inhabiting the Spanish peninsula, spread outwards towards Northern and Eastern Europe and to the Azores. We likewise noticed that the Lusitanian area was invaded by a North African fauna, by a northern and by an eastern fauna. All the evidence I have been able to collect points to the fact that these different invasions are of a much more ancient date than is generally conceded. The chief point of interest, however, lies in the fact that the various waves of dispersal left remnants of their former presence in the country. Some adaptable members continue to spread at present; others recede in the direction which they came from. The study of the Lusitanian fauna has revealed no evidence of an unusual extensive destruction of the ancient southern fauna in Pleistocene times. The African forms came to Spain in Miocene times, and have persisted there to the present day, just as many Lusitanian animals and plants have apparently been unaffected by subsequent changes of climate which are supposed to have supervened after their arrival in the British Islands.

CHAPTER VI.

WE must once more turn back to the north, so as to study the most northerly group of animals and plants in Europe more closely. As we advance northward the fauna becomes less rich in species, but the animals of Scandinavia and their origin offer many suggestive problems. In view of the fact that this peninsula is supposed by many to have been smothered in ice in Pleistocene times, a study of its fauna enhances the interest in the country. For, if that supposition were correct, the composition of the fauna should clearly reveal the fact.

The geological history of the Scandinavian fauna as a whole has never received the attention it deserves, though botanists have been very active in speculating on the derivation of the Scandinavian flora. A few zoologists have expressed their opinions on the origin of the animals at present living in Scandinavia or Northern Europe generally; and these I may quote before discussing the subject somewhat in detail.

Petersen, who describes the Arctic butterflies and moths of Europe in a publication devoted to a knowledge of the fauna of the Russian Empire, expresses his belief that the chief immigration into the Arctic area of Europe was post-Glacial. He thought it must have taken place from Siberia, because the majority of the Arctic species are still to be found in that country. Adopting the current views on the climatic conditions supposed to have prevailed in Europe in Glacial times, he concludes that Central and Northern Europe could not have possessed any butterflies at all during the height of the Glacial period.

What effect the Glacial period had on the earthworms of Northern Europe forms the subject of an interesting paper by Dr. Michaelsen. The fact that no endemic species of earthworms occur north of a line which coincides with the

southern limit of the supposed northern ice-sheet, appears to him significant. His explanation of this fact is that the ice masses destroyed all animal life in Northern Europe, and that ever since, the earthworms are slowly endeavouring to regain possession of the lost territory. The intervening time, *i.e.*, between the end of the Glacial period and the present, must, according to Dr. Michaelsen, have been insufficient for the formation of new species.

As Dr. Michaelsen himself admits, his theory is rather vitiated by the circumstance that the Alps possess many well-marked endemic species of earthworms, although these mountains too have been glaciated. Moreover, there does exist one species which by some is considered endemic to Norway, *viz.*, *Helodrilus norvegicus*. Dr. Michaelsen is doubtful about its being specifically distinct from *Helodrilus constrictus*.

Professor Lönnerberg contends, in an essay on the Red Deer, that it has now been satisfactorily proved by geological evidence that every trace of terrestrial animal life was destroyed on the Scandinavian Peninsula during the Glacial period. Hence the animals now inhabiting Scandinavia must, according to him, be the products of post-Glacial invasions from different sources.

Dr. Kobelt is the only zoologist who considers a survival of the Scandinavian fauna through the Glacial period probable. He refers particularly to the land and fresh-water snails.

We gather from these remarks that there is in Scandinavia, just as in our own country, a wide-spread belief that the question as to the origin of the existing fauna has been finally settled by the geological verdict. The geologists in Scandinavia have come to the conclusion that no life was possible in the country during the Glacial period, and the zoologists mostly submit to this verdict and argue that the complexity in the present disposition of the faunal elements must have arisen subsequently to the Glacial period.

However, quite recently renewed efforts have been made in Scandinavia to examine the problem more critically. Thus Dr. Stejneger, in a review on my former book on the European fauna, expressed the opinion that the small-antlered Norwegian

red-deer arrived in Norway in pre-Glacial times. He does not positively state that it survived the Glacial period in the country itself. But he implies it by his subsequent remark, that the large-antlered Swedish race of deer entered the peninsula from the south at a much later period, while the first came across an ancient land-bridge from Scotland.



FIG. 34.—THE DIPPER (*Cinclus cinclus*), FROM A PHOTOGRAPH OF A LIFE-GROUP IN THE DUBLIN MUSEUM.

Dr. Stejneger likewise suggests that the dipper (*Cinclus cinclus*) (Fig. 34), a well-known bird related to our wren, which frequents the banks of rapidly-running brooks, especially in the hilly districts, had a dual origin in Norway. One variety, whose underside is black, occurs in Western Norway, Scotland, Ireland, and some parts of Southern Europe; and it is quite possible that this might be the relict of an ancient

race which travelled along the western shores of Europe at a time when the geographical conditions were very different from what they are now. The wide range of the genus to which the dipper, or water-ouzel as it has been called, belongs suggests that it is very ancient. Dr. Stejneger, indeed, places the origin and beginning of the dispersal of the dippers at not later than the dawn of the Tertiary era.

Another well-known bird which, I think, has had a dual origin in Europe is the capercaillie (*Tetrao urogallus*). It is widely spread in Northern Asia, and entered the Alpine area presumably at an early pre-Glacial time from the east. About the same time it probably penetrated into Arctic Europe from Asia, and slowly gained possession of Scandinavia, Scotland and Middle Europe.

I also regard the northern char (*Salmo umbla*) as a very ancient form in Scandinavia. The char has two distinct districts of distribution in the peninsula according to Mr. Lundberg, viz., a southern in Central Sweden, and a well-separated northern one forming a broad belt along the Norwegian boundary of the country. The northern districts are inhabited by the Alpine variety (*Salmo umbla alpinus*), while in the southern parts another form (*Salmo umbla salvelinus*) is found. Mr. Lundberg explains the discontinuous range of these varieties by the supposition that the northern form originally came from the west and the other from the south.

Some of the smaller forms of Scandinavian crustacea have recently received a considerable amount of attention from Dr. Ekman. He carefully records their range in the peninsula. He divides them into a number of groups according to their geological age. He considers the Arctic-Alpine section as the oldest. This, he assumes, must have inhabited the Central European Plain and also the southern margin of the Alps during the Glacial period. As the climate grew milder, the members of this section retreated northward to Scandinavia and southward to the Alps. He includes among these a species, which I have had occasion to refer to (p. 56), as having been found fossil

in the northern parts of the British Islands, viz., *Lepidurus glacialis* (Fig. 18). Ekman's suggestion, that it formerly inhabited Central Europe, is based on the fact that it has been met with fossil in the turf deposits of Southern Sweden and Denmark. It now lives, as I have already stated, in the Scandinavian Highlands, in Greenland, Spitsbergen and in Siberia. There is nothing to lead us to suppose that this species extended its range further south than Denmark at any time during the past. The fossil evidence tends to show that it advanced southward and south-westward in former times and that it has now retreated again to its northern home. Similar instances of advances and retreats of animals are recognisable in the fauna of every country. The fossil evidence does not support the contention that this species took refuge as far south as Middle Europe in Glacial times and then returned northward again. It only pushed forth outposts, as it were, as far south as Denmark, to reconnoitre suitable fields for specific expansion.

Dr. Ekman refers to one of his groups of crustacea as being of north-eastern origin. The members of this group do not occur in the southern districts of the peninsula or anywhere else in Europe except in the extreme north. The section includes *Polyartemia forcipata*, *Lepidurus macrurus*, *Eurycercus glacialis* and *Canthocamptus insignipes*. Are we to assume that these have wandered to Arctic Siberia from Central Asia in post-Glacial times, and have since commenced to spread southward again into Northern Europe? If so, they would probably have become extinct in their original arctic centre of dispersion, which is improbable. Is it not much simpler to suppose that these species have never been affected by the Glacial period at all, but have spread in pre-Glacial times from Arctic Siberia into Northern Europe, where they have persisted?

When I referred in a previous chapter (p. 56) to the fact of the reindeer (*Rangifer tarandus*) (Fig. 35) having formerly been an inhabitant of Ireland and the British Islands as a whole, I mentioned that it had reached our area from the north. It still frequents Northern Scandinavia and Russia at present.

Formerly its range extended far into Southern Europe. Its remains have been found by Mr. Boule as far south as the



FIG. 35.—THE REINDEER (*Rangifer tarandus*), FROM THE REPORT OF THE NEW YORK ZOOLOGICAL SOCIETY (by permission of Mr. Madison Grant), WITH A MAP INDICATING IN BLACK THE RANGE OF ITS VARIOUS LIVING RACES. THE PAST DISTRIBUTION IS MARKED IN DOTS.

Riviera in Southern France, and it lived along the northern foot of the Alps and of the Pyrenees. It appears probable that the reindeer appeared in Western Europe before the Siberian

animals invaded our Continent from the east, for none of the latter reached Ireland, while reindeer remains are extremely abundant there. The members of this later eastern invasion did not extend their range as far south as the Pyrenees or Southern France. Along with the Arctic fox, the Arctic hare, the lemmings, and perhaps the willow grouse, the reindeer formed a group of northern species which appeared in Western Europe long before Ireland was separated from Great Britain.

The Arctic fox (*Vulpes lagopus*) (Fig. 36) has at present a very similar range to the reindeer. The white fur is, as a rule, only assumed during the winter. In the summer it generally



FIG. 36.—ARCTIC FOX (*Vulpes lagopus*).

becomes brown or bluish-grey in colour. It is rather smaller than our own fox, and is distinguished from it by its shorter ears and snout.

Two kinds of lemming (Fig. 37) are known from European Pleistocene deposits, and both of them inhabit Arctic Europe and Northern Asia. They are small mouse-like creatures with short tails and heads, and thick fur.

The Arctic hare has already been fully described. It is the only one of this group of Arctic animals which lives in the Alps.

The willow grouse (*Lagopus albus*), though its range, like the mammals just cited, formerly extended to the foot of the Alps, is not found there now.

Now, where did all these Northern animals come from? It is not at all likely that the reindeer originated in Scandinavia, as Bogdanov suggested, though there can be little doubt that it had its ancestral home in the north. Professor Schlosser thinks it is evidently of American origin, while Nilsson, the Swedish zoologist, and also Brandt, maintained that it had come from Northern Asia into Scandinavia. From the fact that antlers are developed in the female reindeer as well as in the male, in distinction to all other kinds of deer, Mr. Lydekker concluded that the species represents the oldest line of existing deer with antlers.



FIG. 37.—NORWEGIAN AND GREENLAND LEMMINGS (*Lemmus lemmus* and *Dicrostonyx torquatus*), PHOTOGRAPHED FROM SPECIMENS IN THE BRITISH MUSEUM (*Nat. Hist.*).

That reindeer remains generally occur in the lower horizons of the Pleistocene deposits on the Continent along with several other Arctic species, has been known for a considerable time past. I think it was Bogdanov, a Russian naturalist, who first drew attention to it, and advanced the theory, that there must have been two distinct dispersals of northern animals to Central Europe—one from the north and a later one from the east. More recently Professor Nehring and Mr. Tsherski again commented on this interesting fact. The former, the well-known author of the steppe and tundra theory, which will be described in a subsequent chapter, concludes that the post-Glacial deposits of Middle Europe show a division into three parts, viz., a

lemming period, a jerboa period, and a squirrel period. Professor Nehring found that the reindeer, the lemmings, Arctic fox and musk ox occurred in the lowest deposits, and therefore belonged to the first period. Of these, it will be remembered, all but the musk ox have been met with in Ireland. By the term "post-Glacial," Professor Nehring meant to convey that the deposits are more recent than the first stage of the Glacial period, but he was uncertain as to their exact age.

The northward expansion of the southern fauna and possibly also the eastward dispersal of the American fauna, appear to have been continued through several geological periods. The invasion of the Arctic fauna and subsequently that of the Siberian one into Europe were evidently of a more evanescent nature, though all of them have left a permanent impression upon our Continent.

Because the northern animals invaded the south of Europe, it is not necessary to conclude that the Arctic regions no longer sufficed for their requirements. It certainly would be wrong to assume that a lowering of temperature forced them to forsake their original home. We have no means of ascertaining that they entirely left their homes at all. But we know that it is not an unusually cold winter which compels animals such as the lemmings to undertake the migrations of which everyone has heard. It is mild springs, followed by dry summers, which have been known to produce the wholesale emigration of vast hordes of these little rodents. A few, however, always remain behind. The exceptional southward expansion of the range of these northern animals in Pliocene and early Pleistocene times may have been due to the extensive subsidences of land in the Arctic region which greatly reduced their habitable area.

The food problem would only have affected the reindeer, which subsists during winter on the so-called reindeer moss (*Cladonia rangiferina*). But this lichen is by no means confined to Arctic Europe. It grows abundantly in our own country, in France, and other parts of Europe. It never reaches the strength and thickness with us that it attains further north, where it often

forms a dense mass nearly a foot in depth. It is quite possible, however, that in Glacial times, when the climate was generally more moist, this lichen grew more luxuriantly in Western Europe, and so enabled the reindeer to obtain a sufficient supply of its favourite diet. In summer the reindeer readily feeds on more succulent herbs.

An invasion of northern species into Europe is by no means confined to Pliocene and Pleistocene times. A careful study of the ants found by Professor Emery in the Baltic and Sicilian amber revealed the fact, as he expresses it, that the Arctic fauna of the period "went down from the north as a host of conquerors,"¹ invading the territory formerly occupied by others. The amber deposits referred to, it will be remembered, are of Oligocene age. This event happened, therefore, when Europe possessed a semitropical fauna and flora.

A few remarks about the Arctic Lepidoptera and their geographical distribution may be made here. The Scandinavian butterflies and moths have formed the subject of some interesting essays. Petersen's views have been alluded to. Scandinavia possesses a large number of species. Even Lapland has as many butterflies as we find in the British Islands. The most noteworthy forms are *Colias hecla*, which occurs in Lapland, Greenland, Arctic Siberia and North America, and *Argynnis chariclea*, which has been taken in Arctic Europe, Greenland, and Arctic North America. Among the moths there are a larger number with a similar range. Thus *Anarta lapponica* is met with in Lapland, Greenland, and Labrador, *Anarta zetterstedti* in Arctic Europe, Greenland, Arctic America, and Mongolia. Many of these butterflies and moths are absent from the Alps, but known from America. We can group them, therefore, among the American element in Scandinavia, to which should also be referred plants such as *Naias flexilis* and *Lobelia Dortmanna*. Two other species of plants recently observed in inter-Glacial bog deposits in Northern and Middle Europe, namely, *Brasenia purpurea*, one of the Nymphaeæ, and *Dulichium spathaceum*, one of the Cyperaceæ, are American

¹ P. 400, *Nature*, Vol. 52.

plants which no longer live in our Continent. They have shared the fate of many members of the American group in becoming extinct with us.



FIG. 38.—*PATULA ROTUNDATA*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

That Scandinavia possesses the remains of a south-western fauna, as well as a flora, is proved by the land molluscs.

I referred in the last chapter to the genus *Arion*, to which

our large brown garden slugs belong, as having originated in South-western Europe, and as having spread from there towards the east. In Scandinavia there are four species of *Arion*, three of them ranging as far as Northern Norway, and one even beyond it into Northern Russia and Siberia. The Lusitanian *Patula rotundata* (Fig. 38), an ancient species, which is even known from French Miocene deposits, likewise occurs in Southern Norway and Sweden. In the north, it is replaced by the Arctic *Patula ruderata*, which formerly extended much further south, and which also occurs in the Alps. Our common garden snail, *Helix nemoralis*, is another south-western species. It is found in Southern Norway and Sweden, and so is *Pupa cylindracea*, while *Balea perversa* has penetrated as far as Northern Scandinavia.

All these occur also in Ireland. They must all have spread along the ancient western coast-line of Europe to Scandinavia, and have persisted there throughout the Glacial period, for we possess no fossil evidence to show that a Lusitanian fauna and flora wandered northward in more recent times through Sweden. They may be looked upon as the dominant types of the group, which have been able to resist the modern changes of climate owing to their adaptability.

Besides these south-western species of molluscs, we have in Scandinavia characteristically Arctic forms, such as *Patula ruderata* (Fig. 39) and *Acanthinula harpa*. The latter has not been found south of Scandinavia, either fossil or recent, except in a single locality, and that is on the Riffel Alp, where it has been noticed in the pine woods at a height of above 6,000 feet. Abroad it inhabits the whole of Arctic North America, and it is, perhaps, from there that it has spread directly into Northern Europe and into North-eastern Asia, at a time when these continents were connected by land with one another. The idea that a species such as this, with its discontinuous distribution and its peculiar habitat among pine forests, could have been driven out of the Arctic regions to Southern Europe, and then have remigrated to the Arctic regions, where the pre-Glacial climate in which it originated was probably temperate, seems to me beyond the range of probability.



FIG. 39.—*PATULA RUDERATA*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

A somewhat similar case is presented by the geographical distribution of the ant *Tomognathus sublevis*, except that it is quite confined to Arctic Europe. There are many others like it. That all these should have emigrated to Southern Europe on the advent of the Glacial period and returned again without leaving a trace of their former presence in the south is unlikely.

This may be an opportune moment to survey the question of survival against non-survival from a botanical standpoint. It will enable us to view the points at issue as they affect the animals and plants as a whole.

Professor Blytt's essay on the immigration of the Norwegian flora during alternating rainy and dry periods is known to a wide circle of readers.

He recognises among the Norwegian plants six different elements or groups, viz., the Arctic, sub-Arctic, Boreal, sub-Boreal, Atlantic, and the sub-Atlantic. Each of these elements is composed of numerous species, and each has left its impression on the vegetation as a whole.

Professor Blytt is of opinion that the Arctic plants might have reached Norway by drifting ice when the country was bare and devoid of a native flora. All other plants, he argues, wandered slowly, and step by step, across connected tracts of country.

Two of these elements are, I think, of special importance, viz., the Arctic and the sub-Atlantic. Among the former, some have a remarkably discontinuous range. For example, *Artemisia norvegica*, allied to our common mugwort, only grows in Norway and Arctic North America, while *Carex scirpoidea*, *Draba crassifolia*, and *Platanthera obtusata* have a somewhat similar distribution, and besides are found in intermediate stations in Greenland.

Professor Blytt assumes that the sub-Atlantic coast plants reached their present position at a time when the whole Scandinavian climate was milder than it is now, and when extensive land connections to the south of Norway enabled the plants to extend their range northward. Thus, he remarks, we can understand why the flora of the coast of Bergen should resemble that of Scotland in such a high degree.

To sum up Professor Blytt's views, he contends that the various elements in the Norwegian flora have immigrated at different times in the post-Glacial history of the country, that the Arctic came first and the sub-Atlantic last of all.

Theoretically, this would have been the course of events if the country had been entirely denuded of its flora by the severity of the climate and by the action of the ice during the Glacial period. For, as I have already pointed out in a previous chapter, we must then assume that the Arctic element of the flora would have first taken possession of the country, and finally the most delicate south-western plants, which would have been driven furthest away by the supposed rigorous climate.

Nearly twenty years later Professor Blytt's views became somewhat modified, especially in regard to the Arctic floral element. Our knowledge of the Arctic flora had in the interval made very rapid strides. He could, therefore, in the more recent essay announce the very suggestive view brought out by recent discoveries, that probably not a single species of the Arctic plants found in Scandinavia is of eastern origin. He concluded that during the Glacial period North-western Europe must have had an American-Greenlandian flora, which was very distinct from the Siberian, and that a land-bridge extended then, or in pre-Glacial times, between Scandinavia, Scotland, the Faroë Islands, Iceland, and Greenland. The distinctness of the North European Arctic flora from that of Siberia seemed to him to indicate that Northern Europe and Siberia were separated by an arm of the sea. Professor Blytt also remarks that there is no evidence in Scandinavia of a mild inter-Glacial period, as has been maintained by many geologists (*cf.* p. 85). The deposits in the peninsula which had been looked upon as inter-Glacial all contain Arctic species of animals and plants.

In his description of the floral history of Sweden, Dr. G. Andersson argues, that all the Swedish plants are immigrants to the country. They came from the south, the east, the west, and north, all of them after the close of the Glacial period. He thinks the fact has been thoroughly established, by fossil

evidence, that the first set of plants which took possession of the bare land was the Arctic. He acknowledges, however, that though Lusitanian plants inhabit Sweden no trace of that flora has ever been observed in a Swedish deposit. The most important plants of this south-western flora which still exist in a few scattered localities are our holly (*Ilex aquifolium*), the purple foxglove (*Digitalis purpurea*), the slender hypericum (*Hypericum pulchrum*), and the English sedum (*Sedum anglicum*), all of which are well-known British species. To this group, too, belong the spignel (*Meum athamanticum*) and the sea spleenwort (*Asplenium marinum*), which are confined to a restricted area in Western Norway.

While professing his agreement with Blytt on all the main points, Prof. A. Schulz urges that the upright vetch (*Vicia orobus*) and about half a dozen other plants must have reached Western Norway, where they occur, by way of the British Islands.

That Scandinavia was actually the home of the Arctic-Alpine flora was first urged by Sir Joseph Hooker. Both Dr. Christ and Prof. Engler, on the contrary, showed, and all the authorities just quoted agree with them, that this flora has originated in many different parts of the world.

Professor Engler and Professor Drude are among those botanists who maintain that even in Scandinavia, Iceland, Greenland, and North America several of the old Arctic plants have persisted throughout the Glacial period. When we come to deal with the Alpine plants and their origin, I shall have some further remarks to make on the Scandinavian flora.

I have already quoted Professor de Lapparent's opinion as to geologically recent subsidences in the Northern Atlantic. He believed that the end of the Pliocene and the greater portion of the Pleistocene periods were marked by extensive series of subsidences in the Northern Atlantic, with the result that Europe and America became severed. From a study of the submarine valleys off the American coast and in the North Atlantic, Professor Spencer inferred that these valleys belong to the general period of Glacial deposits, and suggested that they

had been produced during a geologically recent great elevation of land.

Along with the fresh-water mussel, *Margaritana margaritifera*, the wood louse, *Oniscus asellus*, and perhaps the reindeer, Arctic

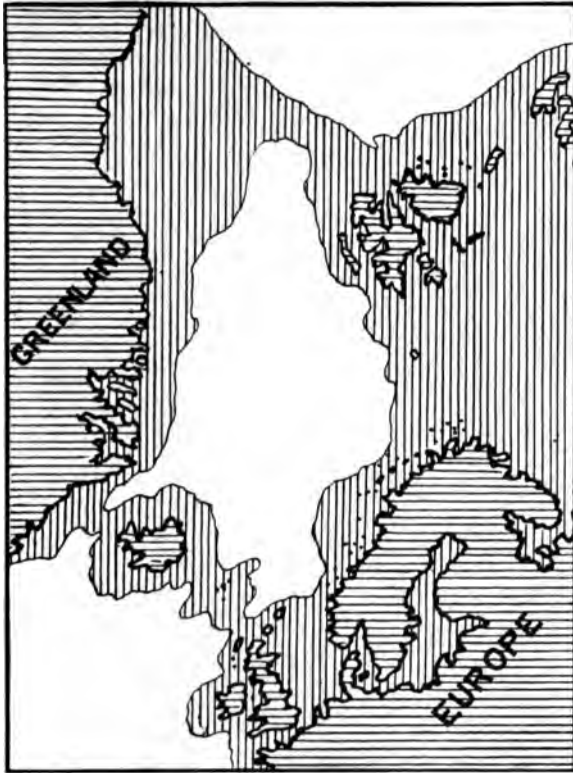


FIG. 40.—MAP OF NORTH-WESTERN EUROPE AND GREENLAND, SHOWING THE ANCIENT LAND CONNECTIONS MARKED IN VERTICAL LINES (STAGE I).

fox, eider duck, and other species, represent the American faunal element in Scandinavia. In a work on the European fauna I assumed on biological grounds that a land connection must have existed in very recent geological times between Northern Scandinavia and Arctic North America, by

way of Spitsbergen and Greenland. This was adversely commented upon by several zoologists. One of them pointed to Dr. Nansen's discovery of a deep polar basin to the east of Greenland, and argued from this fact that my view could not therefore be maintained. But Dr. Nansen's final conclusions, published more recently, in so far as they affect the opinion I expressed on purely faunistic grounds, are that the deep polar basin is probably separated from the deep Norwegian Sea by a comparatively shallow sub-oceanic ridge extending from Spitsbergen to Greenland. His discovery, therefore, does not disprove my theoretical deductions.

I may repeat again what I explained in a previous chapter, that in early Pliocene times, or perhaps during the Miocene period, an extensive continent existed between Northern Europe and Arctic North America (Fig. 40). The southern shores of this continent extended from the British Islands to Newfoundland in a great curve. What is now the Norwegian Sea was then probably the site of a great lake into which drained the rivers from Norway and the lands which extended from that country to Greenland by way of Spitsbergen. The subsidences which took place later converted this lake into a sea like the Mediterranean with a narrow outlet, which may have formed at first between Iceland and Greenland (Fig. 41). This would explain, not only the relationship that exists between the faunas of Iceland and Greenland, but also why so many European forms have reached Iceland without having been able to penetrate to Greenland. Subsequently further depressions of land supervened between the Shetland islands and the Faröes. All this time the northern land communication between Greenland and Scandinavia must have been still available. And it was along the latter that I believe the reindeer and some of the other animals alluded to have invaded Europe in pre-Glacial times.

When Greenland became practically isolated from Europe and America, in the Pleistocene period, the fauna and flora of that country no doubt underwent profound modifications. What species exist there now must of course have survived the Glacial period in Greenland. Only nine different kinds of

land and fresh water molluscs are known from that country, several of them, such as *Succinia groenlandica*, being endemic forms. Even among the moths of Greenland there are several species peculiar to the country.

The view that the fauna and flora at present living in Greenland have survived the Glacial period in that country is not an

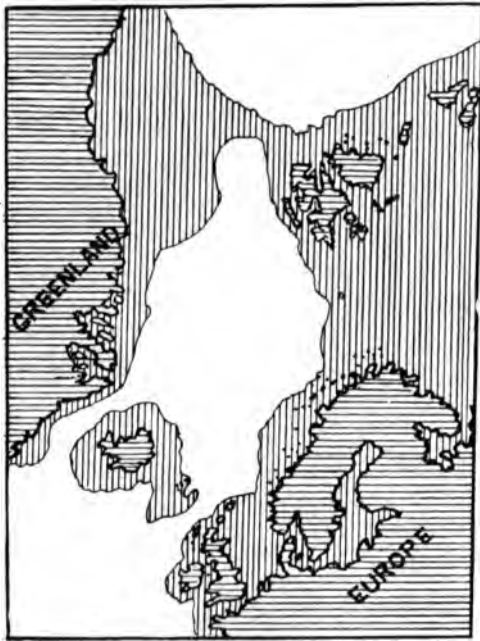


FIG. 41.—MAP OF NORTH-WESTERN EUROPE AND GREENLAND, SHOWING THE ANCIENT LAND CONNECTIONS MARKED IN VERTICAL LINES (STAGE II).

original one. According to Messrs. Wright and Upham, who wrote a little work on Greenland, many species of plants and animals, probably including the reindeer and musk-ox, survived even through the Glacial period on the low shore line and the high *nunataks* of Greenland, which did not become wholly ice-enveloped. Professor Brandt also suggests that reindeer, Arctic fox, musk ox, and lemming, might have survived the Glacial period

in their present habitat. Sir John Hooker and Professor Heer, and more recently Professor Warming, all came to the conclusion that a survival of flowering plants had taken place in Greenland from pre-Glacial times, while Prof. Seward admits that the injurious effects on vegetation of widespread glacial conditions have been greatly overrated.

Before concluding the subject of the Arctic fauna of Europe, a few remarks on the history of the Baltic Sea may not be out of place, as it plays so important a rôle in the origin of the Scandinavian fauna.

Although the Baltic is very poor in the number of its species as compared with the North Sea, it contains a few Arctic forms which are unknown in the latter, and these possess as a rule rather a local range. Thus the fish-louse (*Idotea entomon*) (Fig. 48) occurs chiefly in the eastern portion of that sea. The gephyrean worm *Halicryptus spinulosus*, and the fishes *Cottus quadricornis*, *Liparis barbatus*, and others, have a similar range.

The present conditions of land and water in the Baltic area do not account for these anomalous cases of distribution. We have to take into consideration the geological history of the district. And it appears most natural to connect the presence of these Arctic forms in the Baltic with a former overflow, or transgression, of the White Sea into the Baltic across the lowlands of Northern Russia. Indeed, this was maintained by Lovén and other Swedish naturalists, and also by Dr. Günther. Professor J. Geikie and Professor de Lapparent believe that a wide communication between the Baltic and the White Sea existed in post-Glacial times. Sir Henry Howorth, in an essay on the origin of the Baltic, maintains, on the other hand, that, within recent geological times, it was a fresh water lake, at least the eastern portion of it, and that in the west there was a broad land bridge between Germany, Denmark, and Southern Sweden. When this land connection broke down, marine species entered the area from the west. I quite concur with him as to Scandinavia having been joined to Denmark by a broad land connection, but the fact that some of the most Arctic forms of animal life

should have remained in the northern part of the Baltic and be absent from the west, seems to me to favour the view that there was likewise a marine communication with the White Sea.

One other matter still remains to be dealt with before I conclude this chapter. I have already drawn attention to a remark made by Mr. Crombie, who dwelt upon the great similarity between the Scottish and the Scandinavian floras, and expressed his belief in a more intimate connection in former times between the mountains of Scandinavia and Great Britain.

Professor James Geikie contended that continuous, or nearly continuous land, connecting Greenland with Scandinavia, shut off the cold Arctic currents, and that this post-Glacial land connection accounted for the fact of the similarity of the floras of Spitsbergen, Greenland, Iceland, and the Farøes with the north-west of Europe. Professor Blytt found that not only did the Iceland and Farøe Island floras greatly resemble that of Scandinavia: he discovered that many of the species common to these countries were even attacked by the same kinds of parasitic fungi. Hence he concluded that if an accidental conveyance of the seeds of plants had taken place across the sea, it would be inconceivable that the spores of the fungi should similarly have been thus transported and have alighted so as to enable them to reproduce themselves on their host plants. To explain these conditions of the flora, he favours extensive land connections in pre-Glacial times. "To us the separation of Scotland and Scandinavia," says Professor Judd, "is an event of very recent date indeed; it is not only an accident, but an uncompleted accident! The Scottish highlands, with the Hebrides and Donegal on the one hand, with Orkney and Shetland on the other, must be regarded, to use a technical phrase, as mere 'outliers' of the Scandinavian peninsula." Further on in his address to the British Association meeting at Aberdeen he remarks "that down to post-Glacial times Scotland, and what are now its outlying islands, remained united with Scandinavia." "But

at a very recent geological period, and indeed since the appearance of man in this part of our globe, the separation of the two areas, so long united, was brought about."¹

I think that Professor Judd's views have not found general acceptance among geologists. That Scotland and Scandinavia have long ago formed one continuous land mass can scarcely be doubted, but that this land bridge existed until such very recent times as he assumes does not seem to me probable. A pre-Glacial connection with a survival in several Scandinavian local centres of the Lusitanian and northern elements of the fauna and flora would appear to me to have been the sequence of events, judging from a study of the animals and plants inhabiting the Scandinavian peninsula. More recently, no doubt, Southern Sweden must have been united with Denmark and Northern Germany, as has been pointed out by Sir Henry Howorth, and it is across this land that the country received the large mass of its Central European and eastern animals and plants in Pleistocene times.

¹ P. 1008.

CHAPTER VII.

THE Alps and their fauna, which I intend to describe in this chapter, have much in common with Scandinavia, so much so that the term "Alpine" has often been employed as a synonym for Arctic or northern. I need only cite the indiscriminate application of these terms to our Irish and Scottish hares, on account of their being likewise natives of Arctic Europe, the Alps, and other mountain chains. The conditions of climate and temperature under which animals and plants live in the Alps and in Scandinavia are very similar. Hence it seems natural that the same species of animals and plants should sometimes be found in both of these disconnected areas. Yet the fact that the intermediate tract of Europe, namely, the northern plain of our Continent, should have a different fauna and flora, demands an explanation.

The celebrated Swiss botanist Heer was the first to propound a theory explaining the cause of the similarity of the fauna and flora of Scandinavia and the Alps. The view expressed by Heer, as already stated, was so simple, that it was subsequently adopted by Forbes, Darwin, and many others. It seemed to them to explain the present distribution of the Alpine and Arctic productions of Europe in a most satisfactory manner.

Heer's theory was, that during the height of the Glacial period the animals and plants were driven into the plain of Northern Europe from both Scandinavia and the Alps. There they are supposed to have lived together until the return of a more genial temperature, when they once more retreated to their mountain homes, leaving the plain for subsequent immigrants. During their sojourn in the plain these Arctic and Alpine animals and plants are assumed to have intermingled, so that some of the Arctic specimens retired with the Alpine ones to the Alps, and some of the Alpine specimens receded

northward with Arctic ones. In this manner the similarity between the Scandinavian and Alpine faunas is believed to have been brought about.

At first sight, this does seem indeed a most satisfactory explanation of the origin of the two faunas. But, as in the case of the English and Irish faunas, the Lusitanian element appears to be certainly older in Scandinavia than the eastern one, which pressed into the European plain immediately after the supposed retreat of the Scandinavian and Alpine faunas. The Arctic fauna, too, is clearly older than the eastern in Scandinavia. An immensely long period, with extensive land connections, would have had to elapse after the passing away of the Ice Age to allow all these diverse elements to enter Scandinavia. We are confronted, too, by the question why the Arctic hare should have been driven from the European plain into the mountains on the approach of a more genial temperature, when it flourishes at the present moment in the mild climate of Ireland? Why should the Norwegian lemming, the Arctic fox, and the reindeer not have been dispersed into the Alps, and why should the marmot, the chamois, the Alpine vole, and other mammals of the Alps not have spread to the Scandinavian mountains if they lived formerly in the North European plain?

These are some of the questions which occur to me, and which I submit to show that the suggested explanation of the origin of the Scandinavian and the Alpine faunas still offers a field for further speculations.

If we go back to the dawn of the Tertiary era, to the Eocene period, what are now the Alps then formed a narrow semicircular island in the midst of a great ocean. It was only in Miocene times that the Alpine island became joined by a broad belt of land at its eastern extremity with Asia. It could then receive an assemblage of animals and plants direct from Central Asia. Towards the end of the same period the Alpine peninsula, owing to the partial retreat of the sea on the west, became joined to France. The primitive Alpine fauna, which had developed from an eastern stock, was, therefore, now able to throng into the northern portion of our Continent. The

sea on the northern shores of the Alpine area gradually receded, reducing the ancient ocean, but still leaving a great sea, which rolled between Austria and Southern Siberia, across what are now the Black Sea and Caspian. Meanwhile what had at first been a flat island slowly rose into a mighty mountain chain, such as we see in the Alps at present.

This is a brief account of the geological history of the Alpine area as revealed by a study of its rocks.

The geological history of the Alpine fauna and flora, however, has likewise received some attention. Rüttimeyer was of the opinion that the continuity of generations of mammals throughout Tertiary times until the present period had never been interrupted in Switzerland. A few genera became extinct, yet the survivors maintained themselves within the area of Switzerland to the present day. He does not clearly indicate his views as to the effect of the Glacial period on the fauna of the Alps. Other more recent writers are more precise in this respect. Professor Zschokke, who has specially studied the lake fauna of the Alps, comes to the conclusion that it is composed of a mixture of three distinct elements. He recognises a fragment of an ancient fauna which survived the Glacial period, though he does not suggest that this survival actually took place in the Alps. Another element reached the mountains from the sea by pushing its way up the river courses in post-Glacial times, while the most recent immigrants are the cosmopolitan group of animals which are unaffected by climatic conditions. Neither Professor Nehring nor Professor Studer speak of a possible survival of a portion of the Alpine fauna in the Alps. The latter, however, conveys his belief in the post-Glacial origin of the Alpine animals in his remarks that, with a change of climate, the fauna of the lowlands was gradually pressed to the north and east or ascended the Alps.

Professor Stoll demonstrates the existence in some favourable localities in Switzerland of what he calls "xerothermic relicts of molluscs." He implies that this relict fauna dates from a time when a drier and hotter climate than obtains now

prevailed in Switzerland; and he assumes that this "xerothermic period" must have existed after the Glacial period, as the whole or at least the greater part of the Swiss area had then become uninhabitable for land molluscs. We shall learn later on that similar plant groups inhabit many localities of the Alps or their outliers.

Dr. Kobelt furnishes us with a much more lucid exposition of his views as regards the origin of the Alpine fauna. The molluscan fauna of Middle Europe had developed, according to him, in almost all its details of form and distribution, before the Glacial period began. He came to the conclusion, which I arrived at independently about the same time, that the Alpine mammals are all pre-Glacial, and that the molluscan fauna of the Alps had scarcely an Arctic character at all. There is no proof, he thinks, that the Glacial period had a destructive effect upon the European molluscan fauna. All he admits is a probable emigration from the most unfavourable localities, with a subsequent immigration to them.

Dr. Kobelt was the first to point out to us the distinctive characters of the Alpine molluscan fauna. The genus *Campylæa* (generally regarded as a sub-genus of *Helix*) he looks upon as the most characteristic Alpine group. It is found throughout the mountains and their outliers. No member of the genus occurs in Arctic or even in Northern Europe. The isolated discontinuous range of many of the species on various mountain tops bears testimony against the view that the species have been expelled into the plain or even the Alpine lowlands owing to the action of the Glacial period. Such a distribution as that of *Campylæa* could only have been produced by a very ancient and continued residence of the genus in the Alps. Its occurrence in the Alps is merely an instance of a survival of an ancient group, just as we find similar cases on islands which have long ago become disconnected from continents and have preserved continental relicts after the latter died out in the larger area.

The genus *Pomatias* (Fig. 42) is likewise entitled to be classed among the typically Alpine groups, though some species have pread a little further from the centre of radiation than *Campylæa*.

Some species of *Pomatias* already make their appearance in the European Eocene formation, and persist throughout the Tertiary deposits in forms resembling the living ones. Hence it could not be argued that the occurrence in the Alps of *Pomatias* has anything to do with climate. The genus has been preserved there from early Tertiary times as a relict, in spite of having witnessed the remarkable mutations from a semi-tropical to a semi-Arctic climate.

Zonites is another characteristic snail of the Alpine region, extending south-eastward, like *Pomatias*, and thus indicating



FIG. 42.—*POMATIAS OBSCURUS* (TWICE NATURAL SIZE).

the possible direction from which the genus originally invaded the area.

The genus *Clausilia*, which I have referred to on several previous occasions, and of which four species have been recorded from England, is well represented in the Alps. I have pointed out that from the general range of the *Clausilias* in Europe, both fossil and recent, we can infer that the genus originated somewhere in the south-east, or at least that the active centre of distribution during later Tertiary times was in that region.

We find in the Alps a confirmation of the correctness of this view. In Miocene times the Alpine island as stated above, became

joined to South-eastern Europe. This connection enabled the south-eastern fauna to invade the new peninsula which had thus been produced. *Clausilias* ought, therefore, to occur in abundance in the Alps, as they had henceforth free access to the peninsula from their headquarters. And that is the case. Even in the Western Alps in Switzerland, we still find eighteen species, whereas only three or four species cross the Pyrenees, the greater part of Spain being inhabited by only a single one. The latter (*Clausilia bidentata*) seems to be a much more ancient form than most other Continental species, for it enjoys a wide range in Western and Northern Europe, and occurs as far east as Austria, yet does not penetrate to the Alps. It appears as if its dispersal had originated in the west at a time when the Alpine area was still surrounded by the sea. It will be remembered that the pearl mussel (*Margaritana margaritifera*), which I assumed to have spread to Europe from the north-west (p. 36), has never crossed the coast-line of the ancient sea which once surrounded the Alps. There are many other similar instances.

When Dr. Michaelsen (p. 107) explained the absence of endemic earthworms in Northern Europe by the supposition that they had been destroyed by the Glacial period, he found himself confronted by the contradictory evidence furnished by the Alpine fauna. In the Alps there are a large number of endemic earthworms, such as *Eisenia Udei*, *Helodrilus aporatus*, *H. Ribaucourti*, *H. herculaneus*, *H. lumbricoides*, *H. riparius*, *H. ruber*, *H. asconensis*, *H. tyrtæus*, *Octolasion hortensis*, *O. nivalis*, *Lumbricus melibæus*, and others.

Michaelsen acknowledges that the richness of the endemic Alpine oligochæt fauna militates against the hypothesis of the destructive character of the Glacial period. He suggests that the Alps might not perhaps have been covered by such extensive glaciers as Northern Europe, and that smaller oasis-like districts may have remained unaffected by glacial action.

Most of those who have visited the Alps during the summer holidays have heard of the handsome butterfly known as "Apollo" (*Parnassius Apollo*) (Fig. 43), or have actually seen its graceful movements. It is so abundant in many parts

of Switzerland that the ardent entomologist generally returns with a rich harvest of specimens for his collection. The more experienced naturalist has learned that in the Alps there are,



FIG. 43.—THE APOLLO BUTTERFLY (*Parnassius Apollo*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN EUROPE.

besides the common Apollo, a rarer and more local kind, known as *Parnassius mnemosyne*, and a still scarcer form, confined to the higher regions, called *P. delius*. The first two of these are by no means confined to the Alps. They also occur in Northern

Europe, the common Apollo extending its range southward to the Mediterranean, westward to the Spanish mountains, and eastward right across Asia to Eastern Siberia. All the three species reappear in the Caucasus and in Asia. This geographical distribution would indicate either that they originated in the Alps and radiated out from that centre eastward, or *vice versá*.

A study of the Asiatic fauna, however, has revealed the fact that about forty other species of *Parnassius* occur in Asia. That the genus has originated there is evidenced by the fact that about half a dozen species have spread into the Pacific States of America. The three European species have, in all probability, spread along the old land which in early Tertiary times united the Alpine area with Central Asia. Since that area has become connected with the European plain the more adaptable forms, such as the common Apollo, have somewhat extended their range. That it has spread from the Alps to Arctic Europe is unlikely. I have reason to believe that the Apollo and many other forms of animal life invaded Europe in two separate streams. One went directly westward from its Asiatic centre to the Alps, the other north-westward to Arctic Europe. At any rate, everything indicates that these butterflies are ancient forms which persisted in the Alps throughout the Glacial period.

In the last chapter (p. 117) I alluded to two Arctic species of snails, viz., *Patula ruderata* and *Acanthinula harpa*, as occurring in Northern Europe and appearing again in the higher Alps. Both of these species are likewise met with in Northern Asia. We have such abundant evidence of a dispersal of an Asiatic fauna into the Alpine area across the ancient land alluded to, that we can imagine these two snails to have entered Europe by the two highways which were open to them, one to Arctic Europe, the other to the Alps. We can explain other similar cases of distribution in the same manner.

The belief is rather prevalent that a species living in an Alpine or Arctic country must of necessity be bound to a cold climate. This is not so by any means. The lamellicorn dung beetle (*Aphodius rufipes*), for example, which lives in Siberia, the Caucasus, the high Alps and Arctic Europe, is also known



FIG. 44.—THE CHAMOIS (*Rupicapra ibex*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

from tropical Africa, having been met with on the West Coast of that continent. No less than six other species of *Aphodius* frequent Alpine heights above 7,000 feet. A few ascend the region of permanent snow.

It was pointed out by Dr. Kolbe that of the thirty-four species of dung beetles known to inhabit the higher regions of the Alps, no less than twenty are also found in Arctic Europe. Dr. Kolbe favours Heer's explanation of the origin of Alpine animals; but, as he remarks, most of these twenty species are among the commonest of the dung beetles of Middle Europe, and exhibit, therefore, a continuous range between the Alps and Scandinavia. Only a few show a discontinuous range. It has perhaps escaped Dr. Kolbe's attention that almost all these twenty species are known to inhabit Central Asia as well. To judge from the general facts of distribution, it seems to me more probable that they originated in Asia and then spread by independent routes to Arctic Europe and to the Alps in pre-Glacial times. The enlarged Caspian prevented a direct entry into Eastern Europe from Asia at that time.

I have as yet scarcely dealt with the most important group of Alpine animals, the mammalia. They are particularly interesting.

The best known, perhaps, of all the Alpine mammals is the chamois (*Rupicapra tragus*) (Fig. 44), though, I presume, very few tourists or casual visitors have had an opportunity of watching this graceful goat-like creature in the wild state. Being now rigorously protected, it has of late years become somewhat less scarce in the Alps. In many parts, however, it has died out completely. It occupies quite an isolated position in the European fauna, and is the only species of its genus. Its nearest relations are *Nemorhædus*, to which the Indian serow belongs, and *Budorcas*, another Eastern group. The Rocky Mountain goat (*Haplocerus montanus*), too, is allied to it.

Though a typically Alpine form, the chamois is not confined to the Alps. It is also a denizen of the Pyrenees, the Appennine Mountains, the Dalmatian, Greek and several other eastern mountain ranges.



FIG. 45.—THE ALPINE MARMOT (*Arctomys marmota*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

Considering that all its relations reside in the east, and that its range is just what we might expect from our knowledge of the ancient configuration of the Alpine area, we are justified in the assumption that the chamois has come from the east, probably long before the Glacial period. During the latter time, no doubt, it spread into the plain here and there, but we need not conclude from this circumstance that it became extinct in its centre of distribution and was then reintroduced.

Let us take another instance of a typically Alpine mammal, the Alpine marmot (*Arctomys marmotta*) (Fig. 45). Like the chamois, it is disseminated over several other European mountain ranges besides the Alps, and there is some fossil evidence of its having spread into the plains in Pleistocene times. Its bones have been recorded from several lowland districts. But are we able to discriminate the remains of the Alpine from those of the Russian marmot (*Arctomys bobac*)? I believe most of the bones found in European Pleistocene deposits are referable to the latter species. It formerly invaded the North European plain, and has since retreated to the Eastern parts of our Continent whence it came. The Russian marmot is found right across Siberia as far as the Amur, and there are no less than ten other kinds of marmots in Asia. Asia is consequently the centre of distribution from which the marmots have radiated west and east, for five species have penetrated into Arctic North America. That this took place in pre-Glacial times is evidenced by the fact that one species is known from American Pliocene deposits.

The geological history of most of the Alpine mammals is very similar to that of the chamois and marmot. The Alpine highlands have only a single species of mammal in common with Arctic Europe, namely, the Arctic hare, and it has had quite a history of its own. It probably originated in the Arctic regions, whence it spread all over Northern Asia in pre-Glacial times. Hence it may have entered the Alpine area from the East, along with the species just referred to, or it is possible that it pushed its way into North-western Europe from America, and thence spread across the British Islands and France into the Alps

and Pyrenees in Pliocene times (Fig. 46). It may have reached the other European localities by an independent invasion from the north. A very careful study of the taxonomic and osteo-



FIG. 46.—GEOGRAPHICAL DISTRIBUTION OF THE ARCTIC HARE (*Lepus timidus* = *L. variabilis*).

logical characters of the various races, such as systematic zoologists are now undertaking, will eventually throw light upon this problem.

In the next chapter I propose to describe how a large number

of Asiatic visitors passed into Eastern Europe in Pleistocene times and penetrated as far as the Western parts of the Continent and England. If the Alpine fauna had left the mountains entirely at that time and poured into the plain, it would have mingled with the eastern forms, and both would have wandered to the highlands on the advent of more favourable conditions. Nothing of the kind happened. Of most of the Alpine forms, we have no evidence that they ever lived in the plain, and of that great Asiatic lowland invasion many species returned eastward. Those which remained with us, did not disperse into the highlands.

When we survey the Alpine fauna as a whole, we note that, apart from the old Asiatic stock, we certainly have an admixture of Lusitanian, southern and some eastern forms. These, however, as a rule, are confined to the lowlands. Some, no doubt, have penetrated further upwards. Thus, three species of the south-western slugs, the Arions, still occur in the Western Alps up to 5,000 feet, and so does *Helicella ericetorum*. *Cyclostoma elegans* only penetrates from the south into the valley of the Tessin and in the Western Alps as far as the Lake of Thun. Colonies of southern ants, like *Aphanogaster subterranea* and *Camponotus æthiops*, have been encountered in the cantons of Ticino and Valais. It has been suggested by Professor Stoll that they are the relicts of a post-Glacial xerothermic period (cf. p. 131). I believe that they are pre-Glacial relicts.

That the Alpine area was surrounded by the sea in early Tertiary times, and partially so, as recently as the Pliocene period, can be demonstrated by the fossiliferous strata found on the flanks of the mountains. This evidence is confirmed by that derived from the Alpine lake faunas. Some of these show plainly that their fauna is partially derived from a marine one, and we are on that account justified in applying the term "relict lakes" to these basins.

The Lake of Geneva has yielded quite a number of relict forms. Nemertean worms are almost altogether marine, yet here exists a species known as *Prostoma lacustre*. The turbellarian worms, *Monotus morgiense* and *Plagiostoma Lemani*, belong

to marine groups. Finally, a caprellid—an amphipod crustacean—included in the genus *Podalirius*, has recently been discovered in the lake. All other species of this genus are thoroughly marine forms.

There are other relict lakes on the south side of the Alps. We shall consider these in a subsequent chapter.

Towards the close of the Miocene period, the sea retreated from the western portion of the Alpine area, which became thus joined to France. All the more vigorous and adaptable forms then inhabiting the Western Alps surged down to occupy the uninhabited ground, now the Rhone valley, which was left by the retreating sea. A keen struggle for existence must then have taken place between the mountain species and those already adapted to a lowland life, with the result that the latter remained the masters of the situation. Small colonies of Alpine plants still survive here and there at the base of the Alps, in the plain, as testimonies of their former attempt to gain possession of it.

It is especially boggy ground which forms a stronghold for Alpine plants in the plain, because there they can successfully compete with their more vigorous rivals. A certain number of the lower forms of animal life, among which competition is less severe, have successfully adapted themselves to the plain, where they now flourish as well as in the mountains. Such species frequently range from South-west Asia through the whole chain of the Alps as far as Western Europe. Issuing from the Western Alps, some of these may have joined the Lusitanian fauna in its northward advance. We may explain in this manner the peculiar circumstance that at the present moment we meet with certain Alpine-Asiatic forms mingled with Lusitanian species in the British Islands. A few American forms, which had come at that time into Western Europe, may then have been able to gain admittance to the Western Alps.

In Pliocene times the Rhone valley once more became flooded by the sea, though part of the northern boundary of the Alpine area was in free communication with the northern plain.

Certain adaptable Alpine forms were still able to spread northward into England and Scotland along with such species as had originated meanwhile in the northern plain of Europe.

While the geological history of the Alpine fauna has received as yet comparatively little attention from zoologists, the Alpine plants and their origin, on the other hand, have been keenly investigated for many years. The results obtained by the botanists may serve the useful purpose of substantiating the faunistic evidence.

Just as there are some typically Alpine animals, such as the chamois, the apollo butterfly, and others, that almost every visitor to the Alps has heard of, there are several plants for which these mountains have become famous. I need only refer to the edelweiss (*Leontopodium alpinum*), of which every tourist to Switzerland likes to bring back a specimen. We are accustomed to think that this plant is one of the great rarities, a permanent resident of the snowy regions, which only lurks in inaccessible nooks and corners. But it is by no means confined to the Alps. It grows in the Pyrenees, the Jura, and the Carpathian mountains. Far away in Turkestan, in the Himalayan mountains, in China, and even in Japan our edelweiss appears again. And in the South-western Siberian plain it is one of the common weeds of the meadow. It is absent, however, from Scandinavia.

Little doubt can be entertained that the edelweiss has slowly penetrated to Europe from the south-east and has pushed its outposts to the Alps, and from there to the Carpathians and the Pyrenees, in pre-Glacial times. That this and other Alpine plants are fond of a cold climate is another fallacy. Professor Blytt, whom I have quoted in a previous chapter (p. 120), tells us that in the Botanic Gardens at Christiania the Arctic and Alpine plants endure summer heat well, but they are often destroyed when not sufficiently covered during winter. At Kew Gardens the large collection of Alpine plants have to be wintered in frames, under glass, in order to keep them in good health. Sir Thiselton Dyer expressed the opinion that they are mostly intolerant of very low temperatures. In their native

habitat these plants are protected from the frost in the winter by the natural covering of snow.

So far I have only referred to a single Alpine plant, and there are at least 700 species known to botanists. We are so well acquainted with the general range of these plants, that the whole flora is easily classified into geographical groups.

Professor Wettstein distinguishes four elements in the Alpine flora. The oldest, he argues, originated in Tertiary times from the flora of the European and Asiatic plains. The second element is the northern, the third indicates the influence of a warmer climate, while the fourth consists of the newer variations in plants which have arisen in post-Glacial times.

He explains the similarity of the Alpine and Arctic floras partly by a post-Glacial migration from the Alps northward, and partly by the fact that both the Alps and Northern Europe received plants from the same source, namely, from Central Asia.

Dr. Christ believed that a small part of the Alpine flora originated in Scandinavia and a larger portion in North-west America. The latter portion found its way to the Alps by using Greenland as a stepping stone. The greatest number of plants came, according to Dr. Christ, from the mountains of temperate Northern Asia.

Professor Engler thinks that a great part of the Alpine flora persisted through the Glacial period in the Alps, and that an ancient Arctic element is of Miocene origin. Another element, he supposes, travelled from Central Asia by a circuitous route to the Alps, viz., through Siberia, Arctic Europe, and Scandinavia. Professor Engler recognises the important fact that the Caucasus could not have served as a means of communication between the numerous plants which are common to the Alps and Central Asia, for the Caucasus possesses only ninety-six Alpine species, while the Altai mountains in Asia have 114.

Professor Kerner urges that the mountains of the temperate zone had already in Tertiary times a flora similar to our Alpine one. When the plants were compelled to descend into lower regions during the Glacial period, only very few species from

other parts of Europe joined them in their return to their original habitat.

It is evident then that many of the Continental botanists hold that the Alpine flora is of pre-Glacial origin. But there is a well-known English authority, too, Mr. John Ball, who has made a special study of the subject, and whose opinion is worthy of note.

He remarks that, of the plants which are common to the Alps and the north of our Continent, the larger number do not extend to all the three great mountain ranges of Central Europe. There are forty species common to the Alps and to Northern Europe which have not been found either in the Pyrenees or the Carpathians.

He also draws attention to the fact that during the middle Tertiary period these mountain chains were divided by arms of the sea. What is now Europe was then an archipelago. Ball believed thoroughly in the pre-Glacial origin of the Alpine flora, and expressed his opinion that the effect of the Glacial period, both on the distribution of the plants and on the climate of Europe, had been greatly overrated. While admitting that an increased rainfall, together with a moderate diminution of the mean temperature, had caused an extension of the glaciers of Northern Europe, he did not accept the view that the Alpine plants could have spread across the plain of our Continent.

The conception that the animals and plants common to the Alps and Arctic Europe have arisen independently from an Asiatic centre in late Tertiary times seems to me to agree best with the geographical changes which our Continent has undergone, and of which I propose to give further illustrations in my next chapter.

CHAPTER VIII.

IN the last chapter I discussed the history of the fauna and flora of a great mountainous area in Central Europe of comparatively recent geological origin. Having been isolated from the remainder of our Continent for a considerable time, while open to the influences of Asia, the Alpine area became an Asiatic peninsula in the centre of Europe. The subsequent junction with other faunas produced comparatively little effect on the composition of its original fauna.

The eastern plain of Europe and its animals, which we shall consider now, are in many respects very unlike the western. While the Alpine area had already made its appearance in the Oligocene sea, a great portion of the eastern plain of Europe was still covered by it. What remained of the eastern plain was probably isolated from Asia at that time and open to western influence only. The Caucasus mountains, like the Alps, were just emerging as islands from the great Oligocene ocean.

It seems probable that in Miocene times Arctic Europe was in free communication with Northern Siberia. Part of the eastern plain of Europe may then have received its early Asiatic colonists indirectly from Central Asia. The greater portion of Russia was still covered by the Miocene ocean, as it was subsequently by the Pliocene sea.

Even during part of the latest period in early Pleistocene times an extension of the Caspian Sea stretched far into Northern Russia; and it was only after its final retreat that the great eastern invasion of steppe mammals could have taken place, of which we have evidence as far west as England.

Our knowledge of the Russian fauna is still rather meagre. Many of the works on the zoology of the vast empire of the East, being written in Russian, are inaccessible to the workers in the western states.

It is now about forty years since the Russian zoologist Brandt first recognised the existence of an insurmountable barrier which separated the eastern plain of Europe from Northern Asia in later Tertiary times. In discussing the flora of Scandinavia, I have already drawn attention to it (p. 120); and since Brandt's time his view has been accepted by Professor Boyd Dawkins, Professor Köppen, and others who have dealt with this aspect of the problem of our European fauna.

Taking into consideration the well-known fact that mammoths, rhinoceroses, reindeer, and other large ungulates lived within recent geological times on the shores of the Arctic Ocean in Northern Siberia, Brandt argued that forests and meadows must have extended to these regions, and that the climate must naturally have been much milder than it is now. He believed that this took place at a time when an arm of the sea flooded the land between the Caspian and the Arctic Ocean. The disappearance of this marine channel gradually affected the Siberian climate adversely, and destroyed the northern vegetation, causing the large ungulates to emigrate. As soon as the barrier, which prevented their westward advance, ceased to exist, they were able to pour into Europe.

Professor Karpinski recently reviewed Brandt's theories from a purely geological point of view. He came to the conclusion that an elongated bay stretched southward from the Arctic Ocean for some distance along the eastern flank of the Ural mountains. The Aralo-Caspian basin extended far northward into Northern Russia in Pleistocene times. He does not believe that the northern ocean and the Aralo-Caspian basin were directly joined, except by means of a system of narrow channels or lakes. He assumes, however, that there was a sufficiently free communication between the southern waters and those of the north to have permitted the northern seal and other animals to reach the Caspian. I shall return to the subject of the Caspian fauna later on. It is important meanwhile to remember that we possess an admission from such a geological authority as Professor Karpinski that Brandt's view is supported to some extent by geological evidence.

The author of the work on the present and past fauna of the tundras and steppes, Professor Nehring, does not deal with the origin of that fauna, nor with former geographical conditions. He contents himself with the remark that the fauna of the steppes, which, as he has shown, penetrated from Russia westward, bears the impress of an Asiatic influence.

In a previous chapter I alluded to a copy of Professor Boyd Dawkins's map (Fig. 4) representing his ideas as to the invasion of our Continent by an Asiatic fauna direct from Siberia. Professor Nehring devoted himself for many years to the study of this remarkable assemblage of eastern animals whose remains are scattered over the European plain in Pleistocene deposits. He was the first to recognise that species such as the Russian marmot (*Arctomys bobac*), the great jerboa (*Alactaga saliens*) (Fig. 47), the dwarf pica (*Lagomys pusillus*), some of the susliks, the Saiga antelope (*Saiga tatarica*) (Fig. 51), and many others now inhabiting the steppes of the Volga district in Southern Russia, dwelt in Pleistocene times in Middle and some even in Western Europe. There can be no reasonable doubt that this interesting assemblage of animals, which we may call the Siberian fauna, in distinction to other Asiatic ones already considered, poured into Western Europe from the east. There is no migration that I am acquainted with, which can be so clearly demonstrated from fossil evidence. It is certain, too, that the greater number of the members of this fauna have since retreated to their original habitat. A few, such as the hamster (*Cricetus frumentarius*) (Fig. 25), have not only remained in suitable localities in Middle and Western Europe, but have recently exhibited a disposition, as I shall show later on, to renew their westward progress.

Professor Nehring speaks of these as relicts of the steppe fauna. We are likewise acquainted with certain relicts of a steppe flora in Middle Europe.

Besides the occurrence of this fauna and flora of the steppes, Nehring has demonstrated the former existence in Middle Europe of animals which now live in the tundras of Siberia and the Arctic regions generally. The tundra exists further north than the steppe. It is characterised by the dampness of

its climate, whereas the steppes are dry. The tundra is composed of marshy soil, with a growth chiefly of dwarf birches



FIG. 47.—THE GREAT JERBOA (*Alactaga saliens*), WITH ITS PRESENT EUROPEAN RANGE INDICATED IN BLACK. ITS PAST GEOGRAPHICAL DISTRIBUTION IS MARKED IN DOTS.

and willows, reindeer moss and low-growing plants. It is said to rest on a permanently frozen substratum.

As especially characterising the fauna of the tundra, I might mention the lemmings, the Arctic fox, the Arctic hare and the

reindeer. From the fact that the lemming remains generally occurred deeper down in the Pleistocene deposits, as well as in some caves, than the characteristic steppe fauna, Nehring concluded that the tundra animals inhabited Germany before the steppe animals. He was also led to the belief that the whole of Middle and Western Europe must have had a climate and a vegetation similar to that of the districts which these animals frequent at the present day. In other words, he supposed most of our Continent to have been covered by a vast tundra-like formation.

If we let our thoughts wander back again for a moment to the description given of the Irish fauna (p. 44), it will be remembered that all the animals characteristic of the northern tundra lived in Ireland within comparatively recent geological times. The lemmings and the Arctic fox were probably the first to become extinct in Ireland, the reindeer then followed, while the Arctic hare still resides in the country at the present time. It has become extinct on the continent, except in the high mountain ranges. It enjoys, therefore, the mild climate of Ireland, the Arctic temperature of the tundras, as well as that of the higher Alps, with equal comfort. If this one characteristic tundra species was able to thrive in such climatic extremes, why should not the lemming, Arctic fox and reindeer have done so formerly?

Yet Nehring argued that, because these animals lived in Germany formerly, the country must have been covered with tundras at that time. As I have mentioned, their southward advance was probably due to a contraction of their habitable area through extensive subsidences of the northern lands in pre-Glacial times. There is no evidence that would lead us to suppose that Portugal ever had an Arctic climate, yet the lemming penetrated as far south as that country. In favourable localities, such as Ireland, these Arctic forms no doubt persisted much longer than elsewhere. In Germany, on the contrary, they were swept away by the great Siberian invasion, which, as we have seen, never extended to Ireland. Nehring had observed quite correctly the existence of two distinct

faunas in the German Pleistocene deposits, viz., the older fauna of the tundra overlaid by the newer fauna of the steppe. He had not realised, however, as Bogdanov had done, that these two invasions of Middle and Western Europe originated in widely separate districts.

In a more recent publication, Nehring established that most of the species of steppe animals, which had formerly invaded Middle and Western Europe, still inhabit the "Tshernosem district" of Eastern Russia at the present time. This is the district of the black earth of Russia. It is interesting to note the absence there of all the characteristic tundra species, such as the Arctic fox, Arctic hare and the lemmings, while the reindeer only just enters the district occasionally during its periodical migrations.

This is strictly in accordance with the customary phenomenon in animal dispersal, as I have had occasion to point out more than once. When a wave of new forms enters a district, those that find the latter uncongenial as a permanent residence retire in the direction from which they originally came. The Lusitanian forms, which spread over Europe in Tertiary times, have a tendency to return to the Spanish Peninsula or to become extinct in a south-westward direction. Those animals which entered Europe from the north, like the reindeer, the lemmings and Arctic fox, have mostly receded again to their northern home; and now we have noticed that the steppe forms, like the Saiga antelope, the dwarf pica, the great jerboa and others, have countermarched in the direction from which they pushed into our territory.

To judge from the general range of the steppe group of animals, it is evident that their original home was in Asia. Take, for example, the great jerboa (*Alactaga saliens*) (Fig. 47), which formerly lived as far west as Germany, and is now confined in Europe to Southern Russia. In Central Asia it has a wide range in the steppes and deserts, while eight other species of the genus are found in that continent, and one in Northern Africa.

The European invasion of the steppe fauna from the East

was initiated, according to Professor Nehring, by the advent of steppe conditions in Middle and Western Europe, thus enabling these animals to advance westward.

The problem, however, is by no means so simple; for it has been clearly proved, that in Middle and Western Europe, at any rate, the remains of these steppe animals lie side by side with such as now reside in a tropical or sub-tropical climate, for instance the hippopotamus, the lion and the spotted hyæna. We have also had the experience, within the last few years, of members of the steppe fauna, such as Pallas's sandgrouse (*Syrrhaptes paradoxus*) and the rose-coloured pastor (*Pastor roseus*), having crowded into Western Europe in immense flocks, and having even bred in favourable localities. Some sandgrouse have reared their young as far west as Scotland, where anything but steppe conditions prevail. Hence it is quite conceivable that our western countries might have witnessed invasions or irruptions of other steppe animals on a large scale in former times without any radical change in the climatic conditions having taken place. I shall return to this subject again.

The study of the Siberian fauna has received even less attention than that of European Russia. The difficulty of travelling in Russian Asia makes research there very laborious and costly. A promising young naturalist, Mr. Tsherski, devoted himself for some years to the investigation of the Siberian fauna. Unfortunately for the progress of science, he lost his life in the pursuit of his explorations. Tsherski contended that the problems with which the European zoologist was confronted were much simpler than those which the Siberian naturalist had to deal with. He argued that in Europe we had only to search for the cause of a former displacement of northern animals, such as the reindeer, from Scandinavia to Southern France. In Siberia, on the other hand, a southern assemblage of animals composed of the horse, tiger, deer, Saiga antelope, mammoth and rhinoceros, had invaded the Arctic circle. Tsherski believed that Arctic Siberia supported forests and meadows during the same time that the mountains of Europe were covered with glaciers. A much milder

climate than at present must have prevailed in Siberia during the Glacial period, according to Tsherski. It was only after the Glacial period, he argued, that the climatic conditions became unsuitable for the southern mammals which in Pleistocene times had extended their range northward to the Arctic circle.

Perhaps the great sea-channel which is supposed to have extended from the Aralo-Caspian to the Arctic Ocean formerly may have had some effect in ameliorating the Siberian climate during the Glacial period. It would presumably have conducted the warm waters of Central Asia to the Arctic circle.

It becomes, therefore, a matter of importance, from our standpoint, to ascertain whether there are really any grounds for such a belief.

Professor Karpinski acknowledged the existence of a partial connection by means of lakes or channels between the united Caspian and the Sea of Aral, called the Aralo-Caspian, and the White Sea. But Dr. Sjögren, another writer on the subject, denies that an actual junction between the two seas could have taken place, because Northern Russia must have been covered by ice at the time of the greatest northward extension of the Caspian Sea.

Zoologically, Brandt's view is supported by many important facts. At present the Caspian is altogether an inland sea. It receives the waters of a number of rivers like the Volga, but it has no communication with any larger ocean. Its waters are brackish, because the accession from all its tributary rivers is counterbalanced by the enormous evaporation in that region.

The Caspian seal (*Phoca caspica*) is so closely allied to the northern seal (*Phoca fetida*), which occurs in the Baltic and in the White Sea, that Dr. Nordquist, who specially investigated their cranial characters, scarcely recognises their specific distinctness. It feeds largely on the Caspian salmon (*Salmo salar caspicus*), a variety of our northern species. The fisheries of the Caspian are extremely important, especially at the mouth of the Volga. No less than five different kinds of herring have been distinguished in the Caspian, one of which

is common to it and the Black Sea. This fact alone would seem to point to a recent connection between these two seas. I shall presently return to that subject.

The Aralo-Caspian connection with the Polar Sea in Pleistocene times seems to Kobelt highly problematical, because the molluscan fauna of the Caspian would, in his opinion, show



FIG. 48.—THE FISH LOUSE (*Idotea entomon*).

some traces of it. It is quite possible that the mollusca may not, as a rule, have been able to adapt themselves so well to the brackish water which the Caspian must have maintained, even if connected with the Polar Sea, though the common cockle (*Cardium edule*) is found in the Caspian in a variety identical with that of the White Sea.

Among the crustaceans, the marine isopod, *Idotea entomon* (Fig. 48), known to inhabit the Arctic Ocean and the Baltic, has

also been taken in the Caspian. Two new amphipod crustaceans (*Pseudalibrotus Nanseni* and *P. glacialis*), recently described by Professor Sars, from the Arctic Ocean, are said to be closely allied to Caspian species. The whole genus to which they belong is confined to the Arctic Seas and the Caspian.

Of another genus of amphipod crustacean, called *Pontoporeia*, only two species were hitherto known, one (*P. femorata*) being an Arctic marine species, whereas the other (*P. affinis*) is a fresh water relict form. Recently another species (*Pontoporeia microphthalmia*) has been discovered by Professor Sars in the Caspian. Finally, there occur in the Caspian two shrimps of the genus *Mysis*. When discussing the Irish fauna, I mentioned (p. 27) that a species belonging to this genus, viz., *Mysis relicta*, lives in Lough Neagh, and that it is looked upon as a marine relict form. No less than six species of *Mysis* were known, all from the northern seas, until these two additional Caspian forms were discovered. This alone points to a recent connection of the Caspian with the Arctic Ocean, while I have referred to a good many other facts in distribution which tend to uphold this theory. It is, moreover, supported by Professor Sars and Professor Zograf on zoological grounds.

The crustaceans *Pontoporeia affinis* and *Mysis relicta* just mentioned are called relict forms because they are the somewhat modified descendants of marine species. It is believed that the sea once covered the area where they are now found, and that they are the remnants or relicts of the ancient marine fauna.

On consulting the map of *Mysis relicta* and its geographical distribution in Europe (Fig. 49), it will be observed, that the fresh water lakes in which this crustacean is found—the so-called relict lakes—occur in Ireland, Denmark (Lake Furesö), Northern Germany (Lake Madü, in Pomerania), Sweden (Lakes Wener, Wetter and Mälär), and Finland (Lakes Ladoga, Kallavesi, etc.). It has been suggested that the sea not long ago flooded the land from the north-east; and covering Finland, Northern Germany, Sweden and Denmark, left these relict species as a standing testimony of its former presence in those

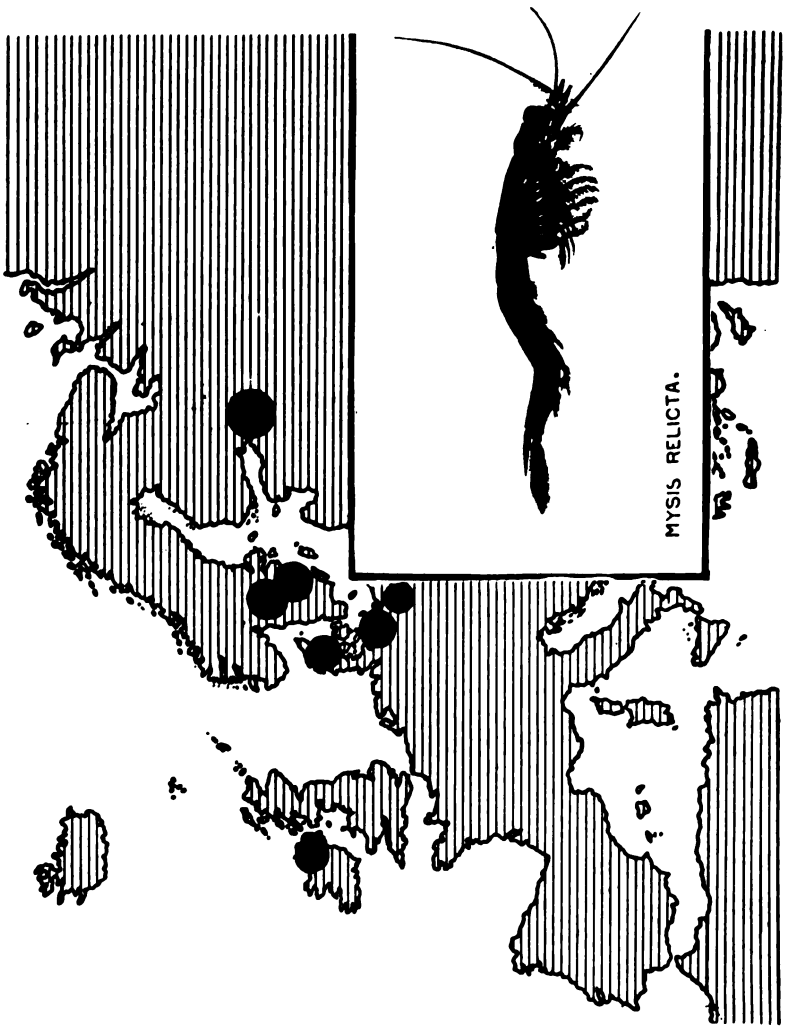


FIG. 49.—THE FRESH WATER SHRIMP (*Mysis relicta*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN EUROPE.

countries. If this transgression of the Arctic Sea across the northern land had joined the Caspian at about the same time, an explanation would thus be furnished of the existence in the latter sea of so many Arctic types of animals.

Quite apart from these northern types, the fauna of the Caspian is full of interest. It contains a large number and a great variety of animals. Since Professor Brussina discovered a number of the peculiar Caspian genera of molluscs, viz., *Caspia*, *Micromelania*, *Zograbica*, and *Limnocardium*, in the Miocene deposits of Croatia, we must look upon the main part of the Caspian fauna as a relict from the old Sarmatic Sea.

Towards the end of the Miocene period a vast sea still extended from Eastern Bavaria across the plains of Hungary and the area occupied by the Black Sea and Caspian to Western Asia. This ocean was entirely distinct from and unconnected with the Mediterranean, and has been called the "Sarmatic Sea."

The pipe fish (*Syngnathus bucculentus*) and the sturgeons of the Caspian are probably Sarmatic relicts. So are certainly the bivalve molluscs just alluded to, as well as *Dreissensia*. All these genera, and even some Caspian species, are known from the Miocene Sarmatic deposits.

In Pliocene times the great inland sea had shrunk to smaller dimensions, but even during the Pleistocene period the Caspian was still joined north of the Caucasus with the Sea of Asov, that north-eastern extension of the Black Sea. The latter was then still unconnected with the Mediterranean, for the Caspian fauna has nothing in common with that of the Mediterranean. It is intimately related, however, to that of the Black Sea. The seaweed *Zostera nana* and many species of fishes and invertebrates which are common to the two seas clearly indicate their recent union.

During all this time the Caucasus must have been quite isolated from northern influences by the marine barrier connecting the Caspian with the Black Sea. And it is interesting to find that this supposition is confirmed by faunistic evidence.

It was Professor Satunin who first recognised that the fauna of the steppes on the northern slope of the Caucasus had

altogether a Transcaucasian or West Asiatic aspect, whereas the animals found in the steppes further north, along the northern shores of the Caspian, are West Siberian in character. Very few of the animals characteristic of the more northern steppes, such as the Saiga antelope, the common hare, and others, seem to have had time to penetrate into these Caucasian steppes. According to Satunin, most of the endemic mammalian species of the Caucasus already lived in that area in pre-Glacial times.

The molluscan fauna of the Caucasus shows the same character as the mammalian one—intimate relationship with Asia Minor and a striking contrast to that of Southern Russia.

In the Caucasus there are no less than eleven endemic species of the genus *Agriolimax*, to which our small white field slug belongs. As might be expected from the fact that the Caucasus had been an island from early Tertiary times and was afterwards joined to Western Asia, it has developed a large number of peculiar genera and species of molluscs. The genera characteristic of the Alps are wanting in the Caucasus, though both these mountain ranges received their original stock of animal life from the same source.

Certain members of far distant faunas which formerly had advanced northward have been left stranded in the Caucasus.

Such, for example, is the operculate genus *Cyclotus* (Fig. 50), residing there in several closely allied species. Although known from European Tertiary deposits, this eastern genus is at present almost extinct in our Continent, the nearest districts where it now lives, apart from the Caspian region, being Central China and the eastern states of India.

It evidently wandered in early Tertiary times to Europe from Southern Asia, and has since retraced its steps towards its original home, leaving a few outposts which might be looked upon as the rearguard of its retreat.

In speaking of the Pyrenean fauna, I called attention (p. 92) to the fact that certain forms seemed more closely allied to Caucasian species than to Alpine ones; for example, the wild goat of the Pyrenees is much more nearly related to that of the

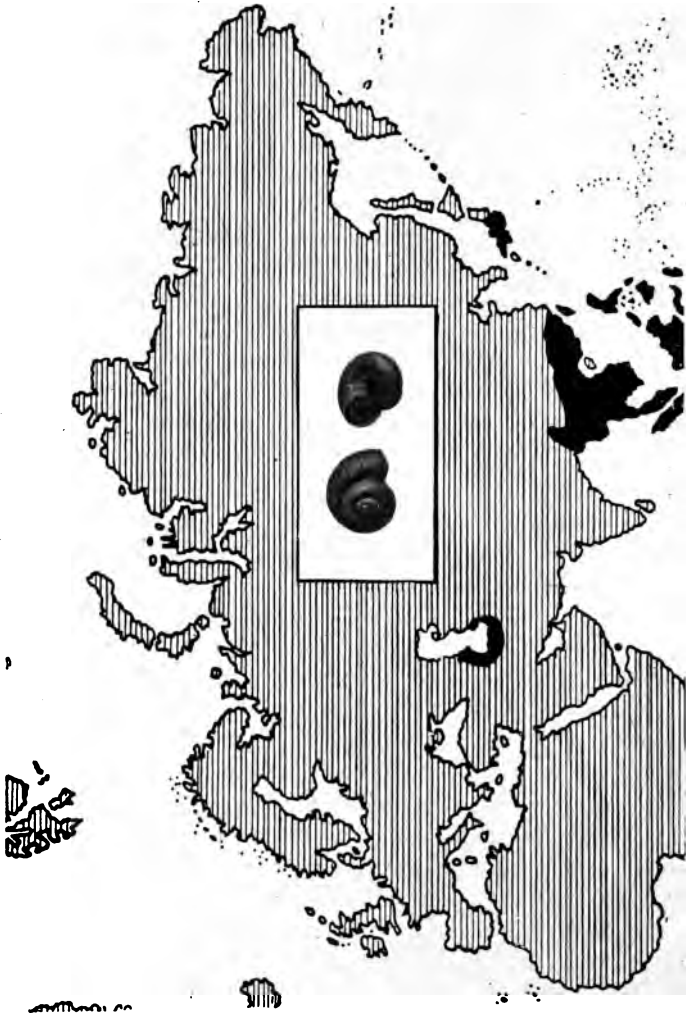


FIG. 50.—CYCLOTUS SIEVERSI, WITH THE GEOGRAPHICAL DISTRIBUTION OF THE GENUS CYCLOTUS.

Caucasus than to the Alpine ibex. Similar instances of an intimate relationship between these two distant mountain ranges occur in all groups of animals. It is evident that our inability to trace the cause of this similarity in the two faunas is due to the former continuous range of species having become a discontinuous one. The Alps could not have served as a route along which these species wandered from Eastern Europe to the west or *vice versâ*. We should, in that case, find some traces there of intermediate forms. The animals could not have wandered from the one mountain range to the other through the North European plain, since the Caucasus was completely isolated from it. Some of the molluscs give us, perhaps, an indication of the path of migration followed. For example, the group *Mesomphix*, belonging to our common genus of snails *Hyalinia*, is confined to the Caucasus, Asia Minor, Crete, the Apennine mountains in Italy, Sicily, North-west Africa, Spain, and Pyrenees. Along this track we find the species of this group, distributed discontinuously, but they indicate clearly an ancient route of dispersal.

It is a well-known fact that the squirrel (*Sciurus vulgaris*), which has an enormous range in Europe and Asia, from the British Islands right across to Japan, is absent from the Crimea, although suitable woods abound in the peninsula. Other forest-loving species, such as the red deer and roedeer, on the other hand, are found in the Crimea. The Crimea for some time formed a peninsula of the Caucasus, while it was surrounded by the sea on all other sides. The geological formation of the Crimea differs somewhat from that of the Caucasus, and it is probable that the two areas were not joined for lengthy periods. Among the more sedentary species, such as the snails and slugs, the faunistic differences between the Caucasus and the Crimea are striking, though these two areas have undoubtedly been connected in recent times. For the Strait of Kertch, which now divides the Crimea from the western prolongation of the Caucasus, is evidently produced by quite a recent subsidence. The Russian naturalist Köppen endeavoured to explain the absence of the squirrel

from the Crimea by the supposition that it had not had time to cross from the Caucasus before the separation took place. He thought the other forest mammals had reached the Crimea in recent times across the frozen Strait of Kertch.

There is no need of assuming any such course of events, however. The squirrel in truth is absent from the Crimea, not because it was unable to travel across from the Caucasus, but, as it has now been ascertained, because it does not inhabit the Caucasus at all.

From later Tertiary times up till quite recently geologically speaking, certainly while man already inhabited the East, the Black Sea was entirely separated from the Mediterranean. The Bosphorus, Dardanelles and Ægean Sea did not exist. But what did exist and has now vanished was a long bay of the Black Sea which extended right across South-eastern Turkey to the north of the Bosphorus and the Dardanelles. The Eastern Mediterranean, as I shall explain more fully later on, crept northward through the subsiding Ægean lands, until it finally broke into the waters of the brackish Black Sea, destroying the Dreissensias and many other remnants of the ancient fauna. Through the greater part of Pleistocene times the Black Sea, while remaining connected with the Caspian, preserved its former independence from the Mediterranean. At the present it may be looked upon as a remote gulf of the latter. A swift current flows out of the Black Sea into the Mediterranean through the Bosphorus, and beneath this a reflux of the Mediterranean waters, charged with its characteristic fauna, enters the Black Sea.

These recent transformations are vividly brought before us when we trace the influence of the Mediterranean fauna on that of the Black Sea. While over 400 species of marine molluscs inhabit the Ægean Sea according to Ostroumov, only 240 are known from the Sea of Marmora, only 150 from the Bosphorus, ninety from the Black Sea, and only fifteen from the north-eastern part of the Sea of Asov.

As no Mediterranean species are known from the Caspian, the connection between it and the Sea of Asov must already

have ceased to exist when these events were brought about. It is worthy of note that one species of the characteristic Caspian genus of lamellibranch molluscs, named *Dreissensia*, had an enormously wide range in Europe and Asia immediately before, or during the early part of, the Glacial period. This species, *Dreissensia polymorpha*, occurs fossil in Western Siberia near the shores of the Sea of Aral, in Russia, Armenia, Germany, and even in France. In later Pleistocene times, it apparently disappeared almost entirely from Europe, except from the Caspian. It is spreading again rapidly north of the Alps, chiefly owing to the presence of canals. Even in England it is now almost ubiquitous, though absent from Ireland. As *Dreissensia polymorpha* is not able to live in pure sea water, the fact of its having become established in England, apparently as an accidental introduction, about the beginning of last century has always been looked upon as an instructive example of the facility with which such introduced species thrive and spread. However, Mr. B. B. Woodward recently discovered this fresh-water mussel in a sandy layer fifteen feet beneath the streets of London, in a deposit which was probably accumulated in the early days of the city's existence. Mr. Kennard found it in a still earlier deposit—in a shell marl near Oxford. These two discoveries seem to indicate that *Dreissensia polymorpha*, as far as the British Islands are concerned, did not become entirely extinct in Pleistocene times, as had been supposed. It probably lingered on in a few secluded spots until the time when canals were constructed in this country, whereby its dispersal was greatly facilitated.¹

Such a gradual westward diffusion of an eastern species is very different from the sudden migrations, or "irruptions," as they have been called, of Pallas's sand-grouse (*Syrrhaptes paradoxus*). The home of this interesting bird is the steppes of Central and Western Asia. Occasionally immense flocks leave their country to search for new pastures. Thus in

¹ The geological history of *Dreissensia polymorpha* has been dealt with in greater detail in my former work on the European fauna.

the year 1859 a number of sand-grouse made their appearance in Europe. Four years later a still larger flock swept across our Continent as far as Western Europe. Then again in 1888 they reappeared, and some members of this last irruption even bred and reared their young in Scotland, under vastly different surroundings of both climate and scenery from what the birds were accustomed to in their Asiatic home. What induces this bird to undertake such extensive migrations is not definitely known. They are probably due to an insufficient food supply at home.

Large flocks of another bird, the nutcracker (*Nucifraga caryocatactes*), occasionally break into Europe from Northern Asia by way of Central Russia. In 1885 one of the most important invasions of the last century occurred. Another took place in 1844. These flights did not extend quite so far west as those of the sand-grouse. The nutcracker has never been observed in Ireland, while it has been met with now and then in both England and Scotland. The sand-grouse is almost entirely an Asiatic species, but the nut-cracker is a well-known resident bird in Europe. It breeds in Scandinavia, Russia, parts of Germany, throughout the Alps and in the Pyrenees. The European residents, however, belong to a different race and are perfectly recognisable from the nut-crackers which periodically invade our Continent from the east. The bill in the Asiatic race is slender, while our European form is thick-billed.

These two species, the sand-grouse and the nutcracker, are perhaps the most striking instances of the periodic invasions of our Continent by Asiatic inhabitants at the present time. I have alluded to them to show that a great exodus from one continent to another may take place without a change of climate. Want of food, the most powerful motor of these emigrations, may have acted in a similar way on the Asiatic mammals which formerly spread across our Continent. Such invasions need not necessarily imply a change of climate.

Although there are a large number of insects which have

ollowed the lines of dispersal of the Siberian mammals and birds across Europe, there is but a single land mollusc, which apparently wandered westward from Siberia, north of the Caspian. This species, *Eulota fruticum* (Fig. 27), occupies quite an isolated position in the European fauna. All its nearest relations are Asiatic, and it has itself a wide range in Northern Asia. In Europe it has the geographical distribution of an animal that might have come with the Pleistocene mammals except for the fact that it has found its way to Northern Italy and far north into Scandinavia. Considering the slowness of its advance, this snail could not have entered our Continent in so recent a time as the Pleistocene period. It must be much older. And, indeed, it occurs not only in the lower Pleistocene of Mosbach, in Germany, but in the English Pliocene Red Crag. It could only have come to us by the same northern route which was used by so many other Asiatic species from Siberia to Arctic Europe in late Tertiary times. A second more recent advance may have been made further south from Asia.

It is impossible to draw a sharp line of demarcation between the eastern and the western plain of Europe. Transylvania and the Carpathian mountains do not come within the sphere of either, but as they are of some faunistic interest, they may as well be considered here.

The Carpathian mountains occupy the south-western boundary of the great eastern plain, and in the angle which they form with the Transylvanian mountains lies Transylvania itself. These mountain chains were part of a large island already in early Tertiary times. Much later, when the sea became reduced in size, this island was joined in the north-west to the European plain, and indirectly to the Alps, but the whole district has till the present time preserved a certain independence of the Alpine fauna which is best seen in the sedentary molluscs. One of the sub-genera of *Clausilia*, viz. *Alopi*a, is almost entirely confined to this area, and while there are many other species of molluscs peculiar to the district, the characteristic Alpine species are mostly absent.

The mammals of the Alps and Carpathians are of more

recent origin, and show a closer relationship to one another than the molluscs do.

Just as we find Siberian animals in Western Europe, or at any rate as we can trace their remains far west, so it is with plants. Owing to the absence or extreme scarcity of fossil remains in later geological deposits, we know only little of the past from that evidence. But we know of many recent examples. The field artemisia (*Artemisia campestris*) grows in England only in a small tract in the counties of Suffolk and Norfolk. In dry or sandy places in Germany it is common; in Scandinavia it only penetrates to the south-east. It is abundant in Russia and Siberia, but absent from Southern Europe. Our spiked veronica (*Veronica spicata*) has a somewhat wider but similar range. An allied eastern species (*Veronica tencrium*) has not crossed either to Scandinavia or to the British Islands. Many characteristic plants, included in the same group, have not even spread beyond Middle Europe, such as *Silene tatarica*, which still grows in Eastern Germany.

There is in the east a steppe flora, just as there is a steppe fauna, closely allied to that of Western Asia. In Hungary we have steppe districts with a flora which is partly derivable from the Russian steppes and partly from the south-east.

CHAPTER IX.

I HAVE dealt in the last chapter with the eastern fauna and its origin, and I attempted to show that Eastern Europe was first populated from the west and north. Only in more recent geological times did an invasion of Asiatic animals and plants take place directly from Western Asia to Eastern Europe. And it was largely of a steppe character. It has been traced as far west as England. The fact that its influence is not felt in Ireland would indicate that the latter was already separated from Great Britain when the steppe fauna reached Western Europe.

I also directed attention to the arrival in Middle and Western Europe of a tundra fauna, no doubt accompanied by a corresponding flora, which dates from an earlier time than the steppe fauna. It manifestly came from the north. We have evidence, as I conveyed, that this tundra fauna crossed the Pyrenees and moved as far south as Portugal.

Lartet was the first to notice the remains of the Saiga antelope (Fig. 51), that conspicuous member of the steppe fauna, in French Pleistocene deposits. However, as he recognised only its horns, he concluded that they had been dropped by ancient hunters, who had procured them in exchange from eastern races of man. Professor Gaudry subsequently referred many cave remains of a sheep-like character to the Saiga, and clearly established the fact that it had lived in France.

More recently Mr. Harlé demonstrated its former existence further south. He particularly investigated the south-west of France with a view to determining the limits of the southern extension of the steppe fauna, with the result that he proved that the river Garonne formed its extreme southern boundary. Besides the Saiga antelope, he discovered the bones of one of the susliks, which were considered by Professor Nehring to

belong to the Asiatic *Spermophilus rufescens*. In a note on these discoveries, Nehring observes that at the time when these steppe animals inhabited the south of France, Europe must have extended further west, or at any rate the prevalent winds must have been different from what they are now, so as to allow the development of steppes in France. Having



FIG. 51.—THE SAIGA ANTELOPE (*Saiga tatarica*)

once assumed that steppes were a necessary accompaniment of a steppe fauna, Nehring was led to conclusions which are unsupported by the general facts of faunal or floral distribution.

We should bear in mind that, though most of the members of the eastern steppe fauna advanced westward and subsequently retreated again, certain species are now resuming their westward advance. The hamster (*Cricetus frumentarius*) (Fig. 25) had formerly pushed as far west as France, and then retreated again. It is now steadily gaining ground in Germany in

a westward direction. The European suslik (*Spermophilus citillus*) is not a true native of the steppes, but it is allied to



FIG. 52.—THE STRIPED HYENA (*Hyena striata*), WITH A MAP OF EUROPE INDICATING IN DOTS THE LOCALITIES WHERE ITS REMAINS HAVE BEEN FOUND, THE AREA MARKED IN BLACK SHOWS WHERE THIS HYENA IS STILL LIVING.

the steppe fauna. It has hitherto not been known west or north of Austria. It is now spreading into Eastern Germany, and a steady western progress is being recorded by Dr. Jacobi, who

quotes other similar instances in his essay on biogeographical regions.

There is a widespread belief, as I explained, that the northern and Asiatic animals which occupied the European plain in Pleistocene times, or perhaps during an inter-Glacial period, took refuge in the Alps when the climatic conditions improved. I have already dwelt on the fact that of the northern animals, only the hare is now found in the Alps, while of the eastern steppe forms which have been proved to have lived, along with the Arctic ones, at the northern base of the Alps at Schaffhausen, none seem to have taken refuge in the mountains.

Apart from the remains of Northern and Siberian types of animals, France has yielded an immense number of interesting fossil mammals. We need not go back to the older Tertiary deposits. The more recent Pleistocene ones are quite sufficient for our purpose.

Among the carnivores, two of the hyænas, now confined to Africa and Asia, have been noticed in French cavern deposits. One of these, the smaller one, has at present a wide range in Asia and also lives in Northern Africa. This is the striped hyæna (*Hyæna striata*) (Fig. 52). Its remains have been met with in an ancient cave deposit in the Pyrenees and in another at Lunel-Viel, in the south of France. It has also been found in the Red Crag in England and in the Pliocene of Val d'Arno, in Northern Italy. It seems to be a strictly western form in its European range, and it may possibly have entered our Continent in Pliocene times from the south-west.

The larger South African spotted hyæna (*Hyæna crocuta*) (Fig. 53) had a very different distribution in Europe. Its remains have been found in numerous French caves and other Pleistocene deposits along with many of our modern common European animals. In England and even in Ireland its bones have been discovered mingled with those of the mammoth and reindeer. From Belgium, Germany, Austria, Bohemia, Poland, and Northern Italy we receive similar reports of the occurrence of the spotted hyæna in Pleistocene deposits, often in company



FIG. 53.—THE SPOTTED HYENA (*Hyaena crocuta*), WITH A MAP OF EUROPE INDICATING APPROXIMATELY THE LOCALITIES WHERE ITS REMAINS HAVE BEEN FOUND.

with eastern steppe forms or with animals still living in Western Europe. The past fauna of the Balkan peninsula is as yet little known, and it is probable that the remains of this and other species will be discovered there. It is obvious that the spotted hyæna came from beyond the confines of Europe. Whether it is really of African origin is somewhat doubtful, since it occurs in Indian Pleistocene deposits, and is closely related to some of the Siwalik Pliocene hyænas. Its remains have also been met with in the Altai caves in Siberia, together with those of the mammoth and other mammals. The past range of this hyæna seems to me one of the greatest puzzles I am acquainted with. From the present distribution of the hyænas we should expect the striped species to have been the commonest of the two in Europe. That the spotted hyæna, whose home is now in South Africa, should have been so very abundant in Europe and certainly contemporaneous with early man, seems surprising. The supposition that it entered our Continent from the south-east is justified from its past range in Europe.

In Pliocene times, the great sea which had previously encircled the Alps was gradually shrinking. This permitted a new set of animals, in fact the larger proportion of our present mammalian fauna, to invade our Continent from Asia Minor when the latter was still connected with Europe. This group is, of course, earlier in date, or we might say, older than the Siberian fauna. It will be more fully described in the next chapter.

Another typically African carnivore, the lion (*Felis leo*) (Fig. 54), came to Europe a little later than the hyæna. It shows the south-eastern origin more clearly. It probably still inhabited South-eastern Europe in historic times. Its remains have been traced from Yorkshire to Eastern Spain, and eastward as far as Odessa, southward to Sicily and Northern Africa. Although its ascertained past range in Europe is perhaps greater than that of the hyæna, the reason for my supposition that the lion arrived more recently is that its remains have not been met with in any Pliocene deposits such as the Forest Bed, and that it has not reached Ireland,

which must then have been already disconnected from England.

In early Pliocene times, the sabre-toothed tiger, an animal



FIG. 54.—THE LION (*Felis leo*). PHOTOGRAPHED FROM SPECIMENS IN THE DUBLIN ZOOLOGICAL GARDENS, WITH A MAP OF EUROPE INDICATING IN DOTS THE LOCALITIES WHERE ITS REMAINS HAVE BEEN FOUND. THE AREA MARKED IN BLACK SHOWS WHERE IT IS STILL LIVING.

with enormously developed canine teeth, took the place of the lion.

There are two other large mammals on whose former occurrence in Europe I have had occasion to comment in

previous chapters. Of these the mammoth has excited perhaps the most general interest.

The mammoth (*Elephas primigenius*) (Fig. 55), as we know from



FIG. 55.—RESTORATION OF THE MAMMOTH (*Elephas primigenius*). (After Keller-Andree, by permission of Messrs. Fisher & Co.). THE APPROXIMATE AREAS IN WHICH ITS REMAINS HAVE BEEN FOUND ARE INDICATED IN BLACK.

the marvellous wall decorations made by the early races of man in French caves, and from the actual specimens which have been brought to light out of the frozen soil of Northern Siberia had a thick coating of hair. The mammoth is evidently of Asiatic origin, being very closely related, and

possibly the direct ancestor of the Indian elephant. It was a member of that southern fauna, which pushed its way as far as the Arctic circle in Northern Siberia, and even crossed the Bering Strait to North America when that continent was still connected by land with Asia. In Europe it had a very wide range. The caverns and river deposits present us with the bones of the mammoth in enormous abundance. It must have lived in Europe during countless centuries from Ireland in the west to the extreme east of Russia, and to Spain and Central Italy in the south. The form of elephant described from Asia Minor as *Elephas armeniacus*, is said to be intermediate in type between the mammoth and the Indian elephant.

The theory advanced by Professor Falconer, Professor Boyd Dawkins, and Sir Henry Howorth, that the mammoth came to Europe in Pliocene times, is supported by the fact of its occurrence in Scotland and Southern Germany in pre-Glacial clays, and in the caves and river gravels of Ireland.

We have yet to consider another large mammal, the hippopotamus (*Hippopotamus amphibius*) (Fig.26) whose presence in Europe is perhaps more worthy of notice than all other southern types, because it throws more light upon climatic conditions than the others do. We can imagine the lion, hyæna, and elephant adapting themselves to a cold northern climate, for lions, as I have mentioned, have been successfully reared in the open in the British Islands without protection during the winter. But the case of the hippopotamus is different. It seems to require an equable climate, with open water, during summer and winter. From the fact of its remains in Europe being found mixed with those of Siberian and even of northern origin we must infer that it existed on our Continent during the Glacial period. It is significant that no remains of the hippopotamus have ever been met with either in Eastern Europe or in Siberia. In Southern Germany, at Mosbach, near Mainz, it has been found associated with the mammoth and with many species still living in Europe.

We are as yet almost unacquainted with the fossil mammals of South-eastern Europe, but it is extremely probable that hippopotamus remains will be found there. Even at the

beginning of last century it still frequented the Nile in Lower Egypt. It evidently travelled along the Nile valley on its way to our Continent. How it crossed the Mediterranean



FIG. 56.—MAP OF EUROPE, INDICATING IN VERTICAL LINES THE PAST RANGE OF THE SAIGA ANTELOPE, AND IN DOTS, THAT OF THE LION. THE PRESENT GEOGRAPHICAL DISTRIBUTION IS MARKED IN BLACK.

I shall endeavour to explain in the next chapter (p. 193). Whether the Mosbach deposit in Germany in which the hippopotamus has been found is pre-Glacial has not been definitely established, but our Forest Bed in which it occurs

certainly is. The species consequently first colonised our Continent in Pliocene times.

When we examine the maps of Europe showing the past range of the south-eastern animals, of which we might take the lion as an example, and of the eastern steppe animals, of which the Saiga antelope may serve as a representative, what strikes us is the sharp diagonal line of the northern boundary of their range (Fig. 56). This boundary line corresponds closely with the southern limit of the northern drift and erratics, which is generally supposed to agree with the maximum southward extension during the Glacial period of a northern ice sheet. It is not my intention to discuss the geological problems of the Ice Age, as I intimated before. I only draw attention to the fact that a powerful and apparently insurmountable barrier existed at the time the rhinoceros, the lion, the hippopotamus, the hyæna, and many other southern species as well as the eastern steppe forms such as the Saiga antelope, the great jerboa, the susliks, and numerous others, lived in Middle and Western Europe. Scarcely any of these species have been met with north of this diagonal line except in the British Islands, where a few have penetrated into Ireland and Scotland evidently before the barrier affected these countries.

As some of the species cited already make their appearance in England in the Forest Bed, the barrier, whatever was its nature, existed from pre-Glacial times until the time when these animals retreated towards their original homes. Of the disappearance of this barrier we have evidence in the Scandinavian fauna. Many species of the eastern as well as the south-eastern group remained in the territory which they had conquered in Middle and Western Europe, and spread northward as soon as the barrier referred to had disappeared.

I might once more give vent to the opinion, expressed so often before, that all these advances and retreats of animals could only have taken place in a milder climate than the present. Under less favourable climatic conditions than prevail now the hippopotamus could not have wandered northward, nor could

large herds of ungulates have found subsistence in these islands during winter.

With regard to Nehring's idea of a steppe climate, Dr. Krause argues that steppes have mostly originated by the drying up of saline lakes, and that they are frequently maintained as such by the joint action of climate and of animals in checking vegetation. It is for this reason that steppe-like districts are only local in Germany. They still support a salt-loving flora and fauna here and there and furnish saline wells. Dr. Krause believes that in Europe there were always treeless districts and wooded ones, each with its characteristic fauna and flora; and that the plants and animals bound to the steppes chose for their westward advance treeless regions which were suited to their peculiar mode of life.

As an example of a species which probably entered Europe from the south-east in company with the large southern mammals, but which continued to spread northward after the disappearance of the northern barrier, the European pond tortoise (*Emys orbicularis*) (Fig. 57) may be cited. When Asia Minor and Turkey were still joined, it seems to have crossed into Europe. From the south-east it gradually worked its way into Italy, and northward by the rivers which then no doubt poured their waters into the Pliocene sea of South-eastern Europe. It subsequently radiated westward along the Middle European river courses. Its further progress to the north was no doubt arrested by the northern drift barrier. When subsequently that obstacle disappeared, and Denmark became connected with Sweden, it continued its northward advance to that country and also to England. It has now become extinct in both of these countries where its remains have been preserved in the peat bogs. Fifty years ago it was still common between the river Elbe and the Oder in Germany. Now it is steadily vanishing from North-western Europe. On the other hand, it is gaining ground in the east. It has advanced as far north as St. Petersburg, and is now common in Eastern Europe as far south as the Crimea.

Such instances of distribution as this have been explained

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FIG. 57.—THE FRESH-WATER TORTOISE (*Emys orbicularis*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN EUROPE. MARKED IN BLACK AND ITS PALE RANGE IN WHITE.

by the supposition that after the Glacial period a milder climate prevailed, which induced southern species to travel north only to become extinct again on a subsequent change of climate. When we carefully scrutinise the present range of the pond tortoise, it must be obvious that, whatever causes restrict its dispersal, they can have little to do with climate. For while it is retreating southward in France, and is still common in Spain and Northern Africa, it is spreading in Russia, where the climatic conditions are so different. Beyond the confines of Europe, it occurs in Asia Minor, in Persia, and Turkestan. It inhabits probably a much greater area in our neighbouring continent, for its nearest relative, the North American pond tortoise (*Emys Blandingi*), is only found in Canada.

Other reptiles, as a rule, are not so readily preserved in a fossil condition as tortoises, and we know comparatively little, therefore, of the past history of the snakes, for instance, whose study presents so many peculiar features of interest.

Almost everyone is familiar with the adder or viper (*Vipera berus*) (Fig. 58), not only because it is the only British poisonous reptile, but also because its range extends far north into Scotland. Snakes, as already mentioned, are entirely absent from Ireland.

Since we fortunately find the remains of the viper preserved in the Forest Bed, we know that this snake is of pre-Glacial age in England. It must, therefore, have been in Europe in Pliocene times. In tracing its probable home, we must first ascertain its European distribution.

Commencing with Southern Europe, we note that the viper is absent from Central and Southern Spain, and from Southern Italy and the Mediterranean islands. On the other hand, it is met with throughout Scandinavia and in Lapland, where, together with our viviparous lizard, it constitutes the whole reptilian fauna. In the Alps and in the Caucasus it ascends great heights, while in the plain of Europe, both east and west, it is known everywhere. One would almost feel inclined, from this distribution, to fix the viper's home somewhere in



FIG. 58.—THE VIPER (*Vipera berus*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

Germany, were it not for the fact that it occurs in the Caucasus. This also indicates its presence in Asia Minor. Indeed, it has been observed not only in Transcaucasia, but throughout the whole of Siberia, both west and east, and even on the island of Sachalin, on the coast of the Pacific Ocean. Hence it seems more probable that the viper is an Asiatic species, which has first entered Europe from the south-east, and later probably direct from Western Siberia.

Although Germany cannot boast of being the cradle of the viper, large portions of that country have been dry land since early geological times. There was ample time for the development of an important fauna and flora which have spread from Germany to neighbouring countries. The pretty little dormouse (*Muscardinus avellanarius*) seems to have originated in Germany to judge from its European range. Similarly, the snail *Arianta arbustorum*, which I have had occasion to refer to several times (p. 65), has the centre of its distribution in the same country. Among other groups of invertebrates, a great many species with a similar range might be quoted.

Attempts have been made to trace certain genera or families of Mollusca through various geological formations, with the object of probing their gradual development and change of form from early Tertiary times. The difficulty, however, of collecting sufficient or suitable material from any one district in Middle Europe has usually proved a serious stumbling-block. The most noteworthy results have been obtained by Professor Boettger, who took for his theme the geological history of the Pupidæ in the Middle Rhine district.

The family Pupidæ, of which we may take our common *Pupa cylindracea* as a representative, is of interest to the geologist from the fact that to it belongs the oldest terrestrial snail known, viz., *Pupa vetusta* of the Carboniferous of Canada.

The principal result of Professor Boettger's interesting study is that he has demonstrated that the distribution of the various species and genera in former periods was essentially different from what it is now.

Let us take for an example the sub-genus *Lauria*, which



FIG. 59.—PUPA CYLINDRACEA, WITH ITS GEOGRAPHICAL DISTRIBUTION.

includes our common *Pupa cylindracea* (Fig. 59). The sub-genus is now peculiarly attached to a maritime influence. It occurs nowhere far from the sea. In Oligocene times a species of *Lauria* lived in the Middle Rhine district. Professor Boettger correctly inferred from this fact that the Middle Rhine district must have had an oceanic climate at that time. We know, indeed, from the Oligocene marine deposits, that both to the north and south of the region in question there was a vast sea. A strip of land remained in the midst of it which extended to South-eastern Europe on one side and South-western Europe on the other. It is extremely instructive to note that the sub-genus *Lauria* has disappeared from Middle Germany since that remote time. But it has formed two new centres of distribution, one in the extreme south-east, the other in the extreme south-west, of our Continent, where the conditions for its further development were suitable. Both *Pupa anglica* and *Pupa cylindracea* are typically Lusitanian species. They have spread north, south, and east along the sea-coast. In the south-east in Caucasia there exists another small, but distinct, group of species which have made but little headway. We can thus trace a dispersal from an original centre to two new ones, the former having since disappeared owing to mutations of land and water.

If we had commenced our inquiries into the geological history of the European fauna with the European plain, we should have found our efforts at unravelling the intricacies of distribution almost hopeless. For here we have to reckon, besides the large indigenous fauna, with an Alpine one, a north-western and north-eastern, a Siberian, a south-eastern, as well as a Lusitanian element, all struggling for supremacy.

Having commenced our enquiries with a simple island problem the task of tracing the various elements to their homes in a continental district is now a much less complex one. Even the heterogeneous composition of the fauna found in the European plain offers no serious obstacles. With comparatively little research, it is possible to arrive at a satisfactory

conclusion as to the geological history of almost any species or group of species.

Hitherto I have dealt but little with birds, as we have so very few fossil remains to assist us with their geological history. By means of a careful comparative study of their minute variations in plumage in the different parts of our Continent, we can gather interesting and useful general information as to their origin. Much of this detailed work yet remains to be done. I am only outlining a rough sketch of the general features of the history of our fauna, and can only draw attention here to a few of the more salient peculiarities. Birds move more freely from place to place than most other animals, and are therefore less useful in elucidating our present enquiries. Yet the gradual course of their advance from one country to another is instructive.

The geographical distribution of the crow family has always exercised a particular fascination on ornithologists. In consequence of the omnivorous propensities of crows, their dispersal differs in so far from that of most other birds, as they manage to find food for their sustenance in almost any country. They are usually hardy and indifferent to climatic influences. Yet the breeding range of the various species is strictly limited to certain definitely circumscribed boundaries.

Let us take as examples our familiar rook (*Corvus frugilegus*), the hooded or grey crow (*Corvus cornix*) (Fig. 60), and the carrion or black crow (*Corvus corone*). The first is common, and breeds throughout these islands. The hooded crow is much rarer in England, and breeds but rarely, while in Scotland and Ireland it is abundant. The carrion crow is fairly common in England, and breeds there, but becomes rarer in the north of Scotland, and in Ireland it is almost unknown. When we follow these three species to the Continent, we notice that our common rook does not breed in South-western or Southern Europe at all, nor in the greater part of Scandinavia, but does so commonly in Eastern Europe and Western Asia, which are so different in climate from the British Islands. It is essentially a bird of the plain.

The grey crow, too, is not known to nest in South-western Europe. Its European and Asiatic breeding range generally



FIG. 60.—THE HOODED CROW (*Corvus cornix*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

is much greater than that of the rook, and extends even into Africa and Persia.

The black crow has the most remarkable breeding range of

them all (Fig. 61). It is the only one of the three which breeds in the south-west, and it is unknown in the greater part of Eastern and Northern Europe, while it becomes abundant again



FIG. 61.—THE BLACK CROW (*Corvus corone*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN THE OLD WORLD.

in Eastern Asia. Its range is therefore somewhat discontinuous. The black crow and the grey crow are close relations.

Judging from the range of these two species, so ably described by Professor Matschie and Dr. Diederich, it looks as if the grey crow had invaded the territory of the black crow and had

divided the hitherto continuous distribution into an Asiatic and a European group. This supposition is strengthened by the fact that the breeding ranges of the two species rarely overlap; where they do they frequently interbreed.

We may not be able to definitely determine which of the two species is the older, but while the black crow has penetrated to North America and has formed distinct varieties or species there, the other has not even reached the New World. The extra-European range of the two species on that account strengthens the assumption that the grey crow is geologically younger than the black crow, and being more vigorous, has been able to invade the territory occupied by the latter. While the black crow, in pre-Glacial times, spread from Central Asia eastward to America and westward to Europe along the Caucasus and other mountain chains as far west as Ireland and Spain, the grey crow probably originated somewhat later from the same ancestor and may have passed into Europe in the extreme north, pushing its way down the Scandinavian peninsula to the British Islands. There it has already ousted the black crow from its ancient haunts in Ireland, while in Germany the latter has been thrust westward across the valley of the Elbe, which now forms a clear boundary between the two species. Southward the grey crow has driven a wedge right through the once continuous range of the black crow, and has penetrated to Asia Minor and North-east Africa.

The rook is evidently a more modern species, having a much more limited range than either of the others. It may have come from Western Siberia with the steppe fauna, although, unlike most members of that fauna, it seems gradually to extend its range in a westward direction at the present time.

There are still a number of features in the faunal aspect of the western plain of Europe which I have not dealt with. The whole river system abounds with problems of geological interest. I shall only briefly allude to a few of them.

The Danube traverses a large area of Middle Europe, which in Miocene times, and to a great extent in Pliocene times too, was covered by the sea. It is of interest, therefore, to examine

its fauna more closely. I have drawn attention to the remarkable fact that we can still trace the ancient marine barrier which prevented Miocene fresh-water species from crossing the shores of the great sea that skirted the Alps. I assumed the fresh-water pearl mussel to have wandered to Europe from the New World along an ancient land connection (p. 34). At present it occurs up to the shores of the ancient Miocene sea of Southern Germany, not beyond it. And yet the valley of the Danube presents a certain relationship to the rivers of North America. I need but quote the family of fishes known as Umbridæ. Only three species belong to it, one of which, *Umbra Krameri*, is confined to the Danube and its tributaries. The other two, known in America as "mud minnows," are found in the United States.

Notwithstanding that the lower parts of the Danube can scarcely be said to belong to the western plain of Europe, they were not included in the last chapter, and may as well be referred to now.

In the territory of the Save and Drave, two tributaries of the Lower Danube, there occur a number of isolated forms of molluscs which are closely allied to, and in some cases identical with, species found in the Levantine lower Pliocene deposits. *Melania holandri*, belonging to the great family of the Melaniidæ, several species of *Lithoglyphus*, *Hemisinus*, and *Neritina*, are undoubtedly relicts of early Pliocene times. *Lithoglyphus fuscus*, *Neritina danubialis*, and *N. transversalis* are species that already lived in the large Pliocene lakes which occupied this district.

Again, in the plain of Hungary there exists at Püspökfördö, what has been described as a sub-tropical oasis. The two species of *Melanopsis* inhabiting the warm springs of the district seem to be related to Slavonian Tertiary forms. There is also a water lily (*Nymphaea lotus*) which reminds us of southern climes, and others which, according to some Hungarian authorities, date from a time when the country had an equable tropical climate.

That all these should have survived the supposed severity of

the climate which, according to many of our geological authorities, reigned over Central Europe during the Pleistocene period, would seem impossible. And there is no evidence of the existence in Europe of a sub-tropical climate in post-Pleistocene times. There are hundreds of similar cases in all groups of animals. Thus Dr. Von Osten-Sacken discovered near Munich a fly allied to our common "daddy-longlegs," a member of the genus *Elephantomyia*. This genus had hitherto been known in Europe only from its occurrence in the Baltic amber, which is of early Tertiary origin and contains a fauna largely related to eastern tropical species. Besides this one from the valley of the Danube only two other recent species are known, viz., one from North America and another from South Africa.

Our common cockroach (*Periplaneta orientalis*) is supposed to have been accidentally introduced in Europe from the East in recent times. But this is not so. It is probably a survival from Tertiary times in Europe, for it certainly lived on our Continent at the time when the turf deposits were accumulated in Northern Germany, where its remains have been met with.

A rather instructive instance of geographical distribution is that of the crayfish, the fresh-water representative and near relation of the lobster. Not long ago it was thought that Europe was inhabited by one kind of crayfish only, called *Astacus fluviatilis*. Now five different kinds of European crayfish have been distinguished, and two more beyond the Caucasus. In America, too, there are five kinds. None are known, according to Dr. Ortmann's graphic account, from Central Asia, but in the extreme east there is a group of four species which are peculiar in so far as they do not resemble the European or American crayfish very closely. The old name *Astacus* has been superseded by a new one. Our English crayfish is now known as *Potamobius pallipes* (Fig. 62). Already when Huxley wrote his celebrated work on the crayfish, he urged that the different European forms of this crustacean had immigrated from the East to our Continent.

He also held, and his opinion is confirmed by Faxon and Ortman, that *Potamobius pallipes*, the West European crayfish, is older than the other species.

The genus to which the European and American crayfish belongs originated probably in Asia. Colonies started east and west from this hypothetical centre of dispersal. The distribu-



FIG. 62.—THE FRESH-WATER CRAYFISH
(*Potamobius pallipes*).

tion of the genus somewhat resembles that of the European pond tortoise; and, no doubt, the chief dispersal took place in Tertiary times, when Central Asia was still covered by a series of large inland lakes. It seems to me that the original European form was not *Potamobius pallipes*, but the mountain species *P. torrentium*, found in the Alps. This may have sent an offshoot into France when the Alpine area became connected with that country, and

thus have developed the characters of our western *P. pallipes*. The latter extended its range from there westward to Spain and Ireland and southward to Italy, Dalmatia, and Greece. Some of the eastern species may have come to us later by a more direct route from Western Siberia.

A few words may be added to this survey of the fauna of the western plain with regard to the botanical aspect of the subject. While zoologists are only now beginning to recognise and record the minuter distinctions among the races which constitute a species, botanists have long ago chronicled and classified the geographical distribution of species and varieties of plants, and have drawn important conclusions from their study. They have, of course, the great advantage of labouring in a more circumscribed field of research.

Professor Wettstein constructed maps indicating the range of all the European forms of some critical genera in such a manner as to enter on one map such species or varieties only whose range did not overlap. The various maps so obtained helped him materially in co-ordinating the numerous forms into several natural groups. One of these groups contained forms whose area of distribution was closely approximated, the characteristic slight differences in the plants being evidently due to climatic causes still existing at the present day. He assumed, therefore, that such a group had originated quite recently. The period of origin of the other forms was approximately determined in a similar manner. By tracing the relationship of the older groups to extra-European ones he determined their geological age and the route of their former advance from various hypothetical centres.

Other authors have treated the subject from a more general point of view. Dr. Schulz maintains that few of our European plants already existed in Miocene times, and that most of them either immigrated to our Continent or developed there since the commencement of the Pliocene period. He contends that the majority of the immigrants came from Asia and North America, and some from Africa. It is particularly interesting to note that Schulz believes in a pre-Glacial plant invasion of Europe from

North America by a direct land connection *viâ* Greenland, Iceland, the Faroës, and the British Islands. He likewise suggests that another route might have existed, *viâ* Greenland, Franz Josef Land, Novaya Zemlya, and Northern Russia (*cf.* p. 63).

Dr. Schulz shows that the origin of these American plants is still recognisable by the fact of their areas of distribution in Middle Europe having south-easterly boundaries. Our water lobelia (*Lobelia Dortmanna*), for instance, which is found in Scotland, Ireland, and Western England, occurs abroad in North America. On our Continent it does not grow further east than Western and North-western Russia. The common bog myrtle (*Myrica gale*) has a very similar range, except that it is found also in North-eastern Asia, having probably crossed the Bering Strait by an ancient land connection between America and Asia.

The same author traces by similar methods the other component elements of the Middle European flora to their original homes. Thus the holly (*Ilex aquifolium*), a Lusitanian species, occurs north-eastward as far as Northern Germany and South-western Norway, though it also penetrates along the shores of the Mediterranean as far as South-eastern Europe. In Pleistocene continental deposits it has frequently been met with, proving that in the Pleistocene period it had already advanced far towards Eastern Europe. At the present time it seems to be slowly receding in a westward direction.

Professor Engler elucidates very clearly his method of research on the geological history of Middle European plants taking the orchid family as an example. The great mass of Middle European plants arrived, according to him, in post-Glacial times, but he admits that species, which are evidently of Asiatic origin, such as the "lady's slipper" (*Cypripedium calceolus*), must have entered Europe early enough to have enabled them to reach England before the latter became isolated from the Continent.

Botanists and zoologists have thus come to very similar conclusions as to the diverse origin of plant and animal groups, although botanists have not the advantages of fossil resources, such as those possessed by zoologists.

CHAPTER X.

WE must once more turn our attention to the East. In the last chapter I discussed the fauna of a large portion of Eastern Europe. The extreme south-eastern corner of our Continent still remains to be dealt with. And as this is perhaps of all parts the most interesting faunistically, I must devote the whole of this chapter to it.

On several previous occasions I found myself obliged to overstep the boundaries of Europe. And I must do so now again, because it is quite essential to the proper understanding of our own European fauna to cast a few glances at that of our neighbouring continents.

No one can fail to be interested in the history of the Dead Sea. Even within the scope of our enquiries, its study yields much that is indirectly of profound importance. The Dead Sea occupies the deepest valley on the face of the earth. And to this fact it is largely due that an abnormally high temperature reigns within its borders, producing an unusual evaporation of its waters. The salinity of the waters of the Dead Sea is six times as great as it is in the ocean. Organic life is consequently almost absent. The shores of the Dead Sea are equally uninviting. The want of drinking water, the prevalence of vapours charged with sulphuretted hydrogen and carbonic acid, the intense heat, and the salt marshes, which do not permit the growth of any vegetation, amply justify the name which has been given to this remarkable lake.

Yet this peculiar configuration of part of Palestine is geologically of quite a recent origin. A study of the geological deposits of the country enables us, according to Dr. Blankenhorn, to conclude that since early Tertiary times Palestine was composed of a series of horizontal strata, without any deep clefts, such as that of the Dead Sea valley. It was only

towards the close of the Tertiary era, in early Pliocene times that the important and eventful changes in the geological history of Palestine were brought about. Dr. Oswald tells us that a post-Miocene line of fracture can be traced southwards from Armenia into the great rift of the Jordan valley and the Red Sea as far as the African lakes Tankanyika and Nyassa. In Syria from north to south long strips of land sank deep into the earth during a series of catastrophes, accompanied probably by terrible earthquakes. These finally left the country in its present state.

When the principal deep valley was first formed, the climate was evidently much more moist than it is now, with the result that the ravine soon began to be filled with the waters which poured down from the neighbouring heights. A long lake was thus produced, whose shores can still be traced about 100 feet above those of the present Dead Sea level, far to the north and south of it. Owing to further dislocations in the strata and climatic causes, the waters of this lake gradually became more and more reduced and charged with salt. The fauna was also impoverished. It was then that the frightful catastrophe occurred, of which we possess so vivid a description in Genesis, by which the cities of Sodom and Gomorrah were destroyed, and probably flooded by the saline waters of the Dead Sea.

These are the main facts revealed to us by a study of the geology of Syria or derived from Biblical history. But a study of the animals of the country enables us to amplify very materially the history so obtained.

As first pointed out by Canon Tristram and confirmed by Dr. Günther and Mr. Boulenger, the river Jordan contains several species of fishes, for instance *Clarias macracanthus*, which are likewise found in the Nile. We may assume that they originally came from Africa to Palestine. In Lake Tsana, the source of the Blue Nile, there occur several fishes, among them a loach (*Nemachilus*), which point with equal force to a former dispersal from Palestine to North-east Africa.

Among land animals, there are so many features implying former favourable conditions whereby an interchange of faunas

between Syria and Egypt was promoted, that it is only possible to allude to a few.

The coney (*Procavia syriacus*), referred to in Biblical history, is not a rabbit, but a hyrax, a peculiar and isolated group of animals, more closely related to the hoofed animals than to the rodents. The whole family of Hyracidæ is limited to Africa, with the exception of the one species found in Palestine. Another well-known African animal which has penetrated into Syria and along the coast of Asia Minor is the chameleon (*Chamaleon vulgaris*).

These are merely a few of the many relicts of the great African invasion, which must have taken place when the vegetation and climate of Asia Minor were very different from what they are to-day. It is a curious fact, as Professor Osborn has pointed out, "that the African Continent as a great theatre of adaptive radiation has not been sufficiently considered."¹ It has been suggested by Professor Gregory that the Red Sea, not long ago, was a great river valley into which the Nile poured its waters, and into which the waters, too, of the great Syrian lake emptied themselves (Fig. 63). Such a geographical condition would quite well harmonise with the remarkable relationship existing between the Syrian and the North-east African faunas.

In drawing attention to the origin of our European hippopotami, Professor Hull surmised that the present Mediterranean might, in Pliocene times, have consisted of a series of fresh-water lakes, with the most eastern of which the Nile and the outlet of the Syrian lake would then have communicated. Professor Gregory's suggestion of the former geographical condition, however, appears to me a more satisfactory one. As we shall gather later on, a continuous land surface, studded with numerous lakes, extended about the same time from Asia Minor to Greece, so that the hippopotamus, which had probably wandered to the Jordan valley from the Lower Nile in Pliocene times, experienced no difficulty in passing into Europe from the south-east. I explained (p. 97) that it had probably come from South-eastern Europe. It was accompanied, no doubt,

¹ P. 56.

by the spotted hyæna, which travelled more quickly and was thus enabled to attain the extreme west as far as Ireland. When its more slowly moving compatriot reached the shores of England, we may suppose that Ireland had already become separated from this country.

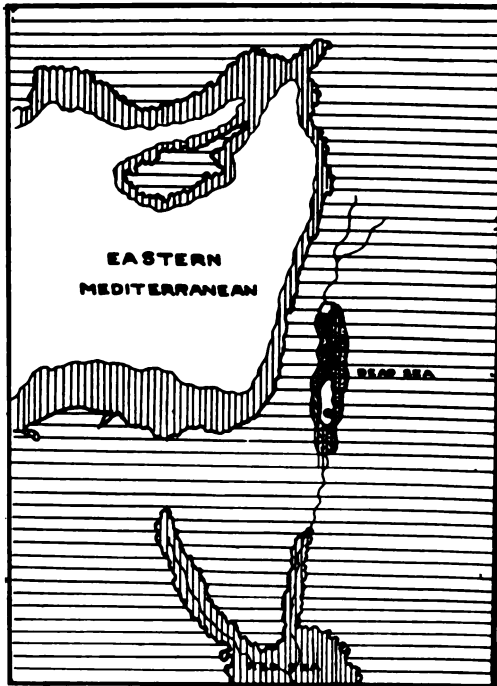


FIG. 63.—MAP OF THE EASTERN MEDITERRANEAN REGION, INDICATING IN VERTICAL LINES THE FORMER EXTENSION OF LAND. THE ANCIENT ENLARGED AREA OF THE DEAD SEA IS MARKED IN DOTS.

Not only the African members of our European fauna, the great wealth of Asiatic animals which have settled down in our Continent, owe their presence in Europe largely to the former land surface between Asia Minor and Greece. An example such as the roe deer (*Capreolus caprea*) will illustrate this. It occurs

from Scotland right across Europe to Greece. Even in Asia Minor, in Palestine and Persia, it turns up again. To judge from the fact that the genus to which it belongs is known from European Miocene and Pliocene deposits, it might be urged that the roedeer is a European species which passed into Asia. It must be remembered, though, that our neighbouring continent possesses three species, whereas we have only one. North and Central Asia as far to the east as China are inhabited by two closely allied roedeer, distinguished from the European species by their larger size and more divergent antlers. On that account, it is more likely that the roedeer originated in Asia. For if it had its home in Europe, its range in our continent would be more extended than it is.

I signified above that some fishes had apparently penetrated to the Upper Nile from Asia Minor. These, I think, were originally Asiatic forms. We have evidence, too, of an advance of European species into East African territory. And it is again especially the highland of Abyssinia which has preserved distinct traces of a European influence.

In Abyssinia lies the southern boundary of the range of the European field-slugs (*Agriolimax*). They reappear there once more in a series of over a dozen distinct forms. The snail *Clausilia*, too, which I have had occasion to cite several times in previous chapters, sent an offshoot from its original European centre to the same country in Tertiary times. Hence we possess abundant testimony of a considerable interchange of species between Europe and North-eastern Africa.

In crossing over the Ægean Sea from Syria to Greece we pass on our way the large island of Crete. It is fully sixty miles from the coast of Greece, and over 100 miles from Asia Minor. Yet the fauna of Crete has a great many species in common with the mainland on either side of that island. The wild goat (*Capra ægagrus*) of Crete can be distinguished from that of Asia Minor, but they evidently belong to the same species. The smaller islands of Antimilo and Joura have wild goats too of their own which exhibit distinct racial characters, but are also offsprings of the Asiatic goat. Hence it is obvious that

Crete and many of the islands in the Greek archipelago must have formed part of the mainland of Asia Minor within recent geological times, for the wild goats of these islands are not recent introductions. Even the Greek coins of ancient Crete were ornamented with the figure of a goat, which is quite recognisable as that of the wild species still inhabiting the island. Aristotle and Cicero have referred to the same animal in their writings, and nothing is known of an artificial introduction in the very earliest historic chronicles.

Not only is the assumption that Crete and the other islands formed part of the mainland of Asia supported by many other facts of animal distribution, there is very strong evidence even that the whole of the Ægean Sea was dry land.

No less than seventy-seven molluscs of Crete out of one hundred and twenty-one inhabiting the island are peculiar to it. About half of these belong to the genus *Clausilia*, so characteristic of South-eastern Europe. With regard to the relationship of these molluscs, it is worthy of note that there is much greater affinity with Asia Minor than with the mainland of Greece. We are justified in concluding from this fact that the island of Crete was connected by land with Asia Minor for a longer time than with Greece.

The geographical mutations of Crete and its neighbouring islands have recently been traced by means of the geographical distribution of snails by Professor Boettger. He indicated that the small island of Cerigotto appertains faunistically to Crete, whereas the island of Cerigo, lying further westward, has stronger affinities with the mainland of Greece than with Cerigotto and Crete. From these facts he deduces that when the Mediterranean broke down the ancient land connection which extended between Asia Minor and Greece, the sea first entered the area between the islands of Cerigo and Cerigotto (Fig. 64). It seems that this took place before Pleistocene times.

An examination of the range of the flightless coleoptera, such as the running beetles, gives us precisely the same results, and proves the correctness of Professor Boettger's views. These insects, inhabiting the Cyclades, the group of islands to the

north of Crete, are almost equally allied to those of Greece as to those of Asia Minor, whereas the running beetles of Crete have greater affinity with those of Asia Minor than of Greece.

The evidence of a dispersal of animal life from Asia Minor, across the Ægean land surface, to Europe is overwhelming. In a previous chapter (p. 75) I alluded to the Roman snail (*Helix pomatia*), (Fig. 24), the largest terrestrial mollusc inhabiting England. I represented that it must have come to us by a slow and steady advance from South-eastern Europe.

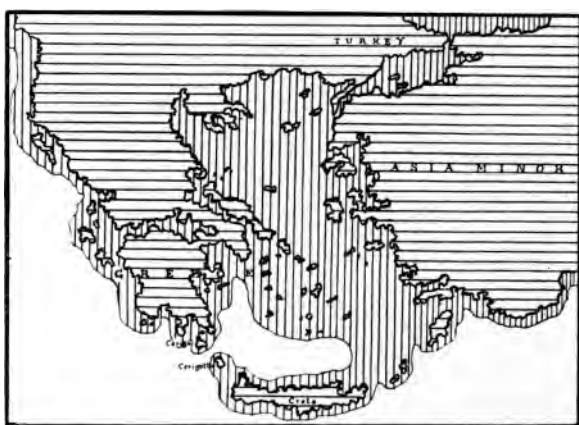


FIG. 64.—MAP OF THE BALKAN PENINSULA AND ASIA MINOR, INDICATING IN VERTICAL LINES THE ANCIENT LAND SURFACE NOW COVERED BY THE SEA.

It does not occur in Asia Minor, but a group of snails to which it belongs are massed together in the land lying between the Ægean Sea and the Euphrates river. From this centre of dispersal new species have evidently arisen, and the more hardy members have struck out for new ground, some going north-west and others westward.

In connection with the geographical conditions prevailing in Central and Eastern Europe in Tertiary times, it is very significant that we have scarcely any evidence in the Ægean region of a corresponding movement of animals from Northern to

South-eastern Europe. As the Alpine area increased in size in Tertiary times there was ample room for additions in this new country for the Asiatic fauna. And when eventually the Central European sea permitted that fauna to occupy the northern parts of our Continent the animals swept across, and many firmly established themselves in the newly conquered territory.

Towards the west the influence of the Asiatic fauna can be followed as far as Spain, as I have shown. And it is probable that some of the earlier dominant Asiatic types spread across Northern Europe from this new western centre of distribution. Many large and strictly terrestrial animals must have proceeded westward from South-eastern Europe. They were thus able to reach the islands in the Mediterranean, which it would have been quite impossible for them to occupy under the prevailing geographical conditions.

The hippopotamus is not a strictly terrestrial animal, since it spends the greater part of its existence in lakes and rivers. But as it could not obtain suitable food in the sea, and has never been met with in any but fresh waters, we must presume that a land surface with lakes and rivers is necessary for its dispersal.

I have suggested that the common African hippopotamus forced its way from the south-east in Pliocene times to Europe, and also to North-west Africa, and subsequently became extinct there. There are, however, several other forms of fossil hippopotami known from Southern Europe. *Hippopotamus Pentlandi* occurs in the cave deposits of Sicily and Malta. Several allied forms have been described from the Pliocene deposits of Algeria. A dwarf species, known as *Hippopotamus melitensis*, has been met with fossil in Crete and Malta.

We have some evidence, therefore, that probably, in Pliocene times, the continuous land surface, which extended from Asia Minor to Greece stretched far beyond the latter country in a westerly direction. I shall have occasion to return to this subject later on.

When I alluded in a former chapter (p. 109) on the Scandinavian fauna to the water ouzel, or dipper (Fig. 34), a well-known European bird, I mentioned that several races or varieties

of this essentially Asiatic species had been distinguished. The dipper evidently entered Europe from the south-east, one of the branches striking westward into the Mediterranean region. There we still find three closely allied forms, namely, *Cinclus minor* in North-west Africa, *Cinclus sardus* in Sardinia, and *C. pyrenaicus* in the Pyrenees. These have no doubt a common origin, and their range must formerly have been continuous.

Very numerous examples of such species might be brought together which have clearly travelled over a continuous land surface from Asia Minor to the Western Mediterranean region. Not only is this the case with animals. A study of the geographical distribution of plants has elicited the fact that they agree in this respect precisely with the animals.

However, before we turn to another chapter of our enquiries let me mention yet another well-known instance of one of these western migrants.

Everyone is familiar with the common land tortoise (*Testudo graeca*), which is so commonly sold in the East End of London for its accredited virtues in destroying noxious garden pests. It really does not injure the latter, for it is a vegetable feeder. But my object in alluding to it is not connected with its food. Its name of Greek tortoise is well deserved, for it is extremely common in Greece and many of its islands, including Crete. Westwards its range extends into Southern Italy. From there it has crept northward along the west coast. Marine barriers do not seem to have interfered with its progress. It has crossed over to Sicily, Sardinia, and Corsica, and even to the Balearic Islands. It is certain, nevertheless, that the sea does act as a real barrier to its advance, and that it has reached these islands at a time when they were joined to the mainland.

The views which I have propounded as to these former land connections in South-eastern Europe are based purely upon the geographical distribution of the animals found in the Eastern Mediterranean region. But what have the geologists to say on this subject? In the limited space at my disposal I cannot dwell very long on the purely geological aspects of the problem. It may be sufficient to briefly indicate

Dr. Philippson's opinion, as he has summarised the views of other investigators and has himself devoted some time to the study of the geological history of Greece.

In Miocene times, he says, the shores of the Mediterranean Sea skirted the southern coasts of Greece, and extended from there along the Ægean land surface across to Southern Asia Minor. Only towards the end of that period do we find indications of a subsidence of the land both to the east and west of Southern Greece, with a contemporary northward advance of the sea. In the Levantine stage, he continues, sometimes spoken of as belonging to the Lower or Middle Pliocene, the Ionian Islands had become separated from the mainland, while the sea made an inroad into the Ægean continent between the east coast of Greece and the remainder of the old land surface, penetrating towards the neighbourhood of Athens. This was the commencement of the gradually extending Ægean Sea, according to Philippson. Professor Suess, I think, agrees with him in this respect.

Even at the end of the Pliocene period the conditions remained much the same, the Cyclades then forming the northern shores of the Eastern Mediterranean. Only in Pleistocene times—and man no doubt witnessed these tremendous geographical evolutions—did the Ægean Sea overwhelm the old land surface, and finally join the Black Sea by means of the Dardanelles and the Bosphorus. All this agrees, therefore, in all essentials with the results derived from our faunistic studies.

When we cross the Bosphorus from Constantinople to the Asiatic side, and compare the faunas of the two great continents, scarcely any difference is noticeable among the animals. Dr. Kobelt goes so far as to say that, from a conchological point of view, both the shores of the Bosphorus as well as the Dardanelles belong to Asia. The real boundaries between Europe and Asia are to be looked for further north in the valley of the Maritza, a river which sends its waters into the Ægean Sea. It is of interest to note that Dr. Apfelbeck has been able to confirm Dr. Kobelt's contention with regard to

is this south-eastern boundary of Europe from a study of the
is beetles of that region.

We possess geological testimony for the belief, as already
is stated (p. 161), that for some time during the later periods of
is the Tertiary era the Black Sea extended westward into what is
is now the northern portion of the Ægean Sea, without, of course,
is communicating with the Mediterranean. This would explain
is the remarkable circumstance, pointed out so clearly by Dr.
is Kobelt, that many of the molluscs of Asia Minor, found on the
is European side, do not cross the valley of the Maritza.

The Tertiary marine barrier, which thus checked the mol-
luscan fauna advancing from Asia, is still plainly discernible.
Like the barrier in Southern Spain which I alluded to (p. 91),
its effects on the fauna have not been destroyed, as might be
expected, by subsequent movements of animals in Pleistocene
times. If our northern fauna had been driven into Southern
Europe during the Glacial period, as has been maintained,
and then swung back again, surely such records of more ancient
dispersals would long ago have vanished.

I have not made any reference to the scorpions in any of
the previous pages, because they are not found in Central
or Northern Europe. They are an important group in eluci-
dating former geographical changes, as Mr. Pocock observes,
because they are mostly of a fair size and well known. They
are considered to be dependent for their dispersal on continuity
of land. They are, moreover, not particular as to their food, and
are not obliged to follow any certain direction to obtain sustenance.

Of the large scorpions included in *Buthus*, an Ethiopian and
Asiatic genus, several species occur in Syria and Palestine.
Only one (*Buthus gibbosus*) reaches Asia Minor, and it is also
found in Greece and on several of the islands in the Ægean
archipelago. A genus, comprising a number of small species
of scorpions (*Euscorpius*), is almost peculiar to the Mediter-
ranean region. Here we notice again that the Ægean Sea does
not constitute a barrier to this dispersal. Some species have
evidently passed from Europe to Asia before the present
geographical conditions were brought about.

The earwigs and their allies, belonging to the order Orthoptera, constitute another group, which I have scarcely dealt with before. They have much greater facilities for occasional or accidental dispersal than the scorpions, and yet most of the species are bound to a land surface, and are, on that account, of use in our enquiries. Several species of earwigs, included



FIG. 65.—THE PRAYING INSECT (*Mantis religiosa*).

in the same genus as our British form, inhabit Greece and Turkey, and also Asia Minor. But there is a genus of earwig which is almost confined to Asia, one species only penetrating to Europe. This species (*Anechura bipunctata*) lives in Asia Minor, Armenia, and other eastern countries. Apparently at a rather remote time, perhaps in the Miocene period, it crossed to Europe and entered the Alpine area, where it now occurs

in the high Alps. More recently it may have spread from there into Hungary and Russia.

Allied to the earwigs are the leaf insects, one of which habitually assumes such a reverential attitude as to have received the name of the praying insect (*Mantis religiosa*) (Fig. 65). Almost all the species of Mantis are either African or Asiatic. The common praying insect is found all over Southern Europe and Northern Africa, as well as in Asia. From South-western Europe it manifestly turned northward into France, Western Switzerland, and Southern Germany.

While the sea was gradually pushing its way northward, breaking down the Ægean continent, in Pliocene times, the Balkan peninsula, in fact the whole area now buried under the Ægean Sea, was largely covered by a series of fresh-water lakes. These favoured, no doubt, the northward extension of such species as the hippopotamus. Here and there ancient relict forms of Mollusca have been discovered in lakes which, in all likelihood, date from these remote times. The lake of Ochrida, in Albania, has recently furnished quite a number of peculiar molluscs, which probably survived there from Tertiary times, among them several new genera, such as *Chilopyrgula* and *Ginaia*.

For the molluscs especially the Balkan peninsula must be looked upon as an important centre of distribution. If we take a glance at the map indicating the range of *Clausilia* in Europe (Fig. 66), we notice that the Balkan peninsula contains most of the species. Many of them have radiated out from there into the neighbouring countries.

Of the whole of the peninsula, Dalmatia, lying on the north-east coast of the Adriatic, deserves our most earnest attention. Not only does it contain no Pliocene deposits, and has, therefore, been a land surface certainly since Miocene times, but its fauna includes many most interesting forms, principally among the molluscs and beetles. In the next chapter evidence will be brought forward of the relationship of Dalmatia to the countries lying to the west of Italy. Its want of affinity with Italy itself, except the south, is rather a striking character



FIG. 66.—MAP OF EUROPE, INDICATING IN BLACK THE RANGE OF THE GENUS *CLAUSILIA*. THE FIGURES IN THE WHITE CIRCLES REPRESENT THE NUMBER OF SPECIES FOUND IN THE VARIOUS DISTRICTS.

and is a feature characteristic of the whole of the Balkan peninsula.

Italy, with its rather meagre endemic fauna, practically did not exist in the Pliocene period. It is quite a new country. What did appear of Italy above the waters of the Pliocene sea was a long and narrow promontory of the Alps, the crest of the Appennine mountains. The Adriatic, on the other hand was largely dry land. The whole region of the Italian lakes and the valley of the Po was under water. It has been urged by Dr. Peschel that the Italian lakes should be regarded as the fjords of the Pliocene sea of Northern Italy. Other authorities claim that the lakes are of glacial origin. Near Como sheets of fossiliferous Pliocene marls are intercalated between ancient glacial moraines. This gave rise to the supposition that Alpine glaciers had existed in Pliocene times and had deposited their moraines into these fjords of the Pliocene sea. These views have more recently been abandoned, because the character of the Pliocene marine fauna denoted the existence of a warm sea. It seems to me, nevertheless, that the older conception agrees better with the whole of the faunistic development of Europe that I have endeavoured to describe. Indications are not wanting in other parts of the world that the presence of glaciers is not incompatible with a high moist temperature and a semi-tropical fauna. The present fauna, however, of the lakes may be made serviceable in our endeavour to decide which of these two theories is more likely to be the correct one.

It was especially Professor Pavesi who conducted a series of careful researches into the fauna of these lakes, and drew attention to their relict character. The most remarkable of the animals showing a marine origin, first discovered in Lake Garda by Professor von Martens, were the common blenny (*Blennius vulgaris*), a marine shallow-water fish, and the crustacean *Palæmonetes varians*. The latter does not now exist in the Mediterranean at all, but probably found its way there with many other northern species, such as our Norway lobster (*Nephrops norvegicus*), which still occur there. Hence the fauna

of the Italian lakes supports the view that they are the remnants of the Pliocene sea which formerly covered that part of Italy.

About midway from the north to the south of the Adriatic Sea, between the coast of Dalmatia and Mount Gargano, in South-eastern Italy, there exists a chain of small islands right across the sea. South of these islands the Adriatic is deep, while it is shallow to the north of them. These islands still possess a rich fauna, and there can be little doubt that in Pliocene times they formed the northern coast-line of the Adriatic which is a more modern formation.

The fauna of the Appennine mountains is essentially Alpine in character. Even the chamois and other well-known characteristic species are found far away from the Alps in the mountains of Central Italy. South of Naples we gradually meet with another fauna, and the Alpine influence disappears. Somewhere in the neighbourhood of Naples the long narrow Alpine peninsula came to an end, and was separated in Pliocene times by sea from another land mass, which lay to the south. Calabria, the peninsula of Italy which projects towards Sicily, formed part of this more southern land mass, which must have been connected with Dalmatia in the north and with Sicily in the south.

I shall support these statements by additional faunistic evidence in the next chapter, because all this portion of Europe likewise forms part of the western half of the Mediterranean, which will then be considered. The relationships of the fauna of that region generally, will likewise be more fully dealt with in the concluding chapter.

That the Mediterranean was divided into two parts, separated by a land bridge in Pliocene times, has been maintained by some geologists. Others, among them Professor Hull, are of opinion that there were three basins communicating with one another by narrow channels. The zoological evidence is, on the whole, in favour of the former view, although the study of the marine fauna has not yet given us any definite results in support of either theory. But the range of the edible

fresh-water crab (*Potamon edulis*) (Fig. 67), for example, clearly implies such a division of the Mediterranean into two parts. This crab, which belongs to a purely fresh-water family, is abundant in Greece, Southern Italy, and Sicily, and again on the southern side of the Mediterranean in Tunis and Algeria. The immigration of the fresh-water crab into Southern Europe took place during the later stages of the Pliocene period. This would place the origin of the Mediterranean Sea as we now find it in the Pleistocene period, quite a recent event in the geological history of Europe.

As might be expected, the Eastern Mediterranean terrestrial fauna presents some rather striking differences from the Western. The former was, for a considerable time, under the influence of an immigrating Asiatic fauna, while the west had, as we have seen, quite an independent centre of distribution.

Dr. Attems has drawn attention to the fact that there is no group in which this dissimilarity between east and west is more conspicuous than in the Myriopods, that is to say, the group including centipedes and millipedes. Dr. Kobelt, too, has laid stress on this character from a molluscan point of view.

Yet many animals wandered from the Eastern Mediterranean region to the Western, and *vice versa*. I have quoted some instances already. In middle Tertiary times the great central European sea lay right across the track of the animals coming from the south-east of Europe towards the north-west and from the north-west towards the south-east. The early settlers were obliged, on that account, to take a circuitous route in travelling between North-western and South-eastern Europe.

I shall refer more fully to the botanical aspect of this Mediterranean problem in the next chapter. Among the Mediterranean plants, as among the animals, there are many species with a more or less discontinuous range. I might just mention one instance now because it is a familiar English garden shrub, namely, *Rhododendron ponticum*.

The genus is evidently of Asiatic origin. In Miocene or Pliocene times it spread from Asia Minor into South-eastern Europe and also to the Alps, where we still find a couple of

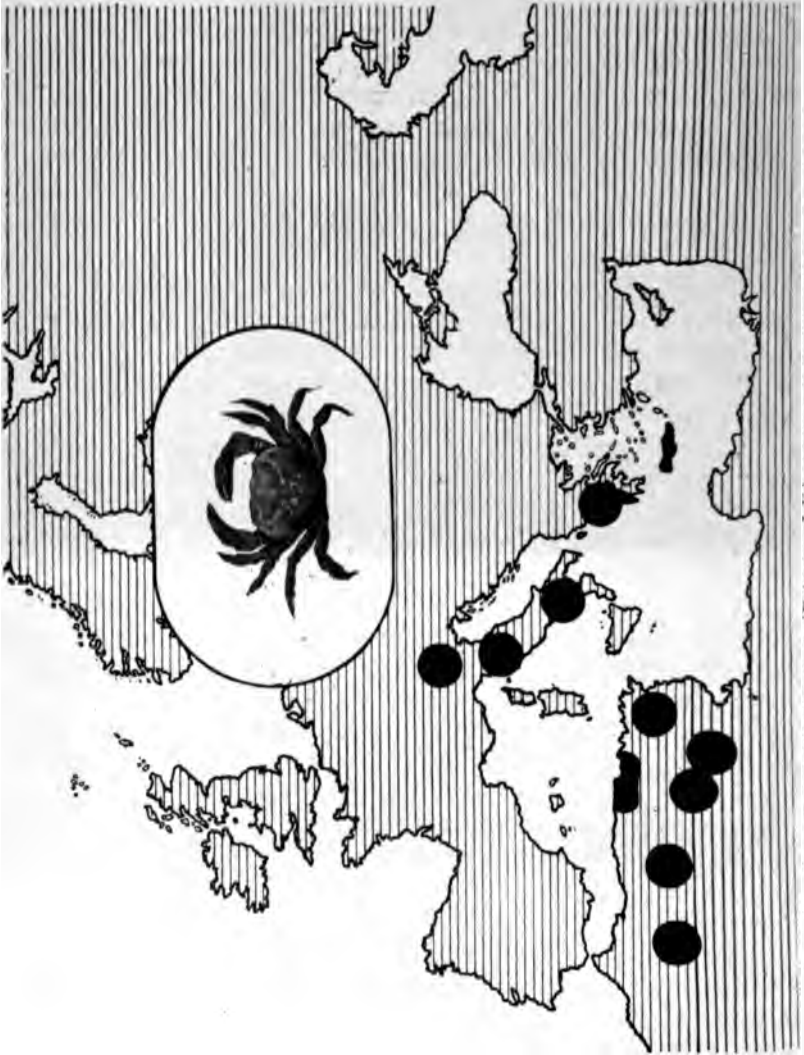


FIG. 67. - THE FRESH-WATER CRAB (*Polimon edulis*), WITH ITS GEOGRAPHICAL DISTRIBUTION.

species which have become modified so as to support the peculiar conditions of Alpine climate.

Other species, no doubt, existed in the Alps formerly. In the so-called inter-Glacial breccia of Höttingen, near Innsbruck, in the Tyrol, the leaves of *Rhododendron ponticum* have been discovered, proving its existence there in Pleistocene times. It has since become extinct in the Alps and in the whole of the Balkan peninsula. Far away to the east, in the Lebanon and in Armenia, it is still met with, and there are small colonies of the same plant in Southern Spain and Portugal. We have here, therefore, an instructive example of a plant which advanced westward and northward, and which only maintains itself in the two extreme boundaries of its range.

CHAPTER XI.

I CONCLUDED my last chapter with a brief account of the recent geological history of the Italian fauna. A good deal more remains to be added. I only indicated the relationship of that fauna with the east. The full story of the western part of the Mediterranean and its islands, and the affinity of their fauna with other parts of Europe and North Africa, has still to be dealt with.

All that existed of Italy in the Eocene period was a small island in the extreme south, which is still part of Calabria. Fortunately the palæontology of the country is fairly well known, and we can thus obtain certain glimpses of the geographical conditions of Southern Europe at that time.

In some of the Eocene deposits of Northern Italy, terrestrial molluscs are abundant. Their presence signifies proximity of land. In the Vicentine series, the genera *Clausilia* and *Pomatias*, two well-known European forms, are already represented. But more than half the species of molluscs exhibit Oriental (Australian) or South American affinities.

The crabs of this deposit tell us the same tale. The crustacean fauna was essentially Oriental, while certain species show relationship with America.

Professor Emery gives us an idea of the insect life of the early Tertiary times from his study of their remains in the Sicilian and Baltic ambers. He informs us that the fauna, not only of the south, but of the whole of Europe, was then Indian or Australian in character.

In Oligocene times, the geographical conditions remained much as they were before. It was only during the Miocene period that the Appennine mountains and part of Sicily appeared above the waters.

Even at the present day the vestiges of this ancient Oriental

and American fauna still persist in the Mediterranean region as relicts of early Tertiary times. In the last chapter I alluded to the praying leaf insect (Fig. 65). A near relation is the stick insect (*Bacillus*) of Southern Europe. It is no doubt another such survival of ancient times. Most of the remaining members of the family Phasmidæ, to which it belongs, are either Oriental or Australian. In the genus *Tudora*, of the Balearic Islands, we have a similar relict with an American affinity, for this operculate mollusc has its next of kin in the West Indies.

Numerous similar examples occur in the flora. The dwarf palm (*Chamaerops*) of Southern Europe, which had still a wide range during the Pliocene period, and is now restricted to a few isolated localities, forms part of an Oriental genus.

During all this time, when Italy was yet in its infancy, so to speak, two large land masses existed, one to the east, the other to the west, of it. The eastern one is now part of the present Balkan peninsula, while the western one is still represented by the islands of Corsica and Sardinia.

When Dr. Forsyth Major investigated the caves of the island of Elba and other islands belonging to the Tuscan archipelago, he was able to confirm the report of the occurrence there of remains of several large mammals, such as the deer, bear, antelope, and horse. It is manifest that these small islands could never have supported such a fauna as this. They must have formed part of a larger land mass within recent geological times.

The difficulty of arriving at a suitable solution to this geographical enigma led Dr. Major to pay some attention to the recent fauna of the neighbouring larger islands of Sardinia and Corsica. He noticed that, while a number of the island mammals were absent from the mainland of Italy, almost all of them seemed to occur in far distant North Africa. Attention has been drawn to the remarkable distribution of the Sardinian warbler (*Melizophilus sardus*) by Professor Giglioli, who states that it only breeds in Corsica, Sardinia, and Sicily. On the mainland of Italy it is only known as an exceedingly rare accidental visitor. Far away in

the west, in the Balearic Islands, however, this warbler occurs again as a resident bird.

A study of the reptilian and amphibian fauna yielded further interesting results as to the geographical affinities of Corsica and Sardinia with other countries. It disclosed the surprising fact that not only was North Africa faunistically related to these islands, but also to Sicily, the Tuscan archipelago, to Spain, and Southern France. The whole of this area seemed to form one faunistic province, which Dr. Major called "Tyrrhenis." The mainland of Italy, with the exception of a few isolated patches on the west coast, did not appear to him to belong to this province. The various parts of this area were probably intimately connected with one another at some former period.

More recent researches have perhaps modified Dr. Major's conclusions in several details. For instance, the Sardinian form of the weasel (*Putorius nivalis boccamela*) is now separated from the other Mediterranean ones, while the hares of Sardinia and Corsica are even looked upon as belonging to distinct varieties of the European hare. But his main conception of the intimate faunistic relationship of the countries referred to has been strengthened by many additional observations.

The Pyrenean newt (*Molge aspera*) is, as I have already stated (p. 94), closely affiliated to the Corsican and Sardinian newts, with which it has been placed in a separate sub-genus.

The painted frog (*Discoglossus pictus*) inhabits Sardinia and Corsica and also the small islands of Giglio and Montecristo. Southward it is found on Sicily, Gozo, and in the whole of North-western Africa, and westward in Spain and Portugal.

A variety of the tree frog (*Hyla arborea*), which has probably come to Europe from the east, has been met with in Corsica, Sardinia, and the island of Elba, and then eastward again in the Greek archipelago, in South-western Asia, and other parts of that continent.

Dr. Major dealt only with the vertebrate animals and the plants. The invertebrates yield results no less interesting than those obtained from the higher groups. It was urged by Professor Simroth that the slug *Limax maximus* in Corsica

exhibited indications of an ancient origin. He suggested an immigration from the north in Miocene times.

Molluscs generally must always be regarded as being of fundamental importance for the decision of problems such as the one put forward by Dr. Major. Corsica and Sardinia, at any rate, to judge from their molluscan fauna, must have been connected with one another until geologically recent times.

All about the Riviera in Southern France small colonies of shells are met with, such as *Helix melanostoma* and *aperta*, *Leucochroa candidissima*, *Cyclostoma sulcatum*, and others, reappearing partly in Sardinia and Corsica, and partly in Northern Africa. These are comparatively strangers on our Continent. They quite support, therefore, Dr. Major's Tyrrhenis theory. Other invertebrate groups with a limited range will be referred to incidentally later on.

From a conchological standpoint Dr. Kobelt looks upon Sardinia and Corsica as part of the Alpine system. He contends that these islands became separated from the Continent in Miocene times, and that they were never since connected with it. The islands, no doubt, have a certain Alpine affinity. This does not, however, necessitate their having been joined to the Alps at any time, because the Alpine fauna itself is essentially Asiatic and South-east European in character. The whole of the Asiatic part of the fauna of Sardinia and Corsica could have reached them by the more southern route by way of Greece and Sicily. The presence in the islands of several species of *Iberus*, a sub-genus of *Helix* characteristic of Southern Italy and Sicily, points, moreover, to a southern land connection.

If the opinion, expressed by several authorities, as to the extreme antiquity of the fauna of these islands, should be substantiated, we could establish thereby the age of the European fauna as a whole. We should be able to discover the precise age of some of the animals inhabiting the British Islands. For in Sardinia and Corsica there occur such species as the field mouse (*Mus sylvaticus*), which has a very wide European range and extends as far north as Iceland (p. 64).

To decipher the many puzzles connected with the geological history of the European fauna, the animals of all the European islands should be studied in their minutest details. It is there that we find the keys to the solution of the most difficult problems, and the relicts of past ages which have long ago vanished from the mainland.

As among the vertebrates, so also among the lower animals, a large number of endemic species occur in the islands of Corsica and Sardinia. All the groups have representatives, and there is no need here to refer to them specially. One example, however, is of particular interest. Europe is occupied exclusively by the family of earthworms, known as the Lumbricidæ, with the exception of one region, and that is the Tyrrhenian province. Here we find the singular genus *Hormogaster*, included in a family otherwise confined to South America and South Africa. One of the species of *Hormogaster* is peculiar to Sardinia; the other has also been taken in a few localities in Western Italy, in Sicily, and in Tunis.

The range of this genus reminds one of that aberrant minute Arachnid *Koenenia mirabilis*, which almost equally resembles a spider and a scorpion, and which is the only species known of the order Palpigradi. This remarkable creature has only been discovered in our Continent on the west coast of Italy, Calabria, Sicily, and in Tunis. It reappears across the Atlantic in the two widely separate localities of Chile and Texas. It is another example of that relationship between Southern Europe and America of which I have mentioned instances already, and of which others will be alluded to (p. 229) before concluding this chapter.

Professor Engler treats of the Tyrrhenis problem from a botanical point of view. A few mountain plants occur in Corsica. Some of these also grow in the Western Alps and in the Pyrenees. But many of the Alpine species which originated in the east and which made their way to the Alps, the Pyrenees, and Appennines, are wanting in Corsica. A land connection during the Pleistocene period with the Alps is not to be thought of, according to Professor Engler, because the number

of Alpine plants in Corsica would, in such a case, be much greater than it actually is. If there had been a former land bridge, he thinks, it must be of a much earlier date. The Appennines, for instance, have a far greater number of Alpine plants than Corsica.

A long list of plants given by Professor Engler contains, as he remarks, only a portion of the extremely numerous Mediterranean plants which grow in most parts of the Mediterranean region, and yet are absent from Upper and Middle Italy. Many are found in the eastern and southern parts of the whole region, but not in Italy at all. Others are exclusively confined to the Spanish and the Balkan peninsulas.

The impression Professor Engler received from a careful consideration of these distributional facts was that a large number of the Mediterranean plants had spread along a line drawn between Asia Minor, Crete, Greece, Sicily, and North Africa. This is much what I concluded from my observations of the geographical distribution of the Mediterranean animals. It indicates what I have urged more than once, that plants and animals are subject to the same laws of dispersal.

From the main line of distribution described by Professor Engler many plants branched off northward to Dalmatia or further. Then again from Sicily they extended into Italy as far as Naples and Rome, and from Tunis across Sardinia and Corsica to Liguria, and finally in the far west from North Africa into Spain and Southern France.

It seems decisive, to judge from the instances of distribution quoted, and from many others which are known, that Corsica and Sardinia were connected by land in early Tertiary times with Provence, in the south of France, and with the Eastern Pyrenees (cf. p. 95). Corsica extended no doubt eastward as far as the west coast of Italy. That connection may have lasted until Miocene times or even later. The shrew-mouse (*Crocidura etrusca*) found in France, Italy, Sicily, and Algeria, is perhaps a survival of that ancient land.

Sicily seems to owe its origin to a fusion of several distinct land fragments. Its geological union with Sardinia is

undoubtedly of old standing. Much more pronounced is the affinity between Sicily and Calabria. The molluscs in the two areas show scarcely any difference, according to Dr. Kobelt.

The mere fact of the occurrence of fossil remains of the same species of hippopotamus (*Hippopotamus Pentlandi*) in the Sicilian caves and those of Malta is suggestive of the former union of these islands. To be able to support a creature of that size, Malta must not only have had a larger area: it must have had lakes and rivers.

This hippopotamus was not the only sign of a continental fauna that Professor Leith Adams discovered on the island of Malta. He also unearthed the bones of a dwarf or pigmy hippopotamus (*Hippopotamus melitensis*), which has since been met with fossil in the island of Crete, thus indicating an eastern origin, as I explained in the last chapter (p. 200). All these remains occurred together with those of two peculiar kinds of elephant, and the shells of molluscs still living on the island. The large extinct Pliocene mammals were evidently surrounded by invertebrates and perhaps by many of the smaller forms of mammals, which survived the gradual and extensive geographical revolutions in the Mediterranean area. The range of the porcupine (*Hystrix cristata*) (Fig. 68), which lives in Southern Italy, Sicily, and North-west Africa, would seem to indicate that such is actually the case.

We are acquainted with such a great number of instances pointing to a close relationship between the animals of Sicily, Malta, and Tunis, that there can scarcely be any doubt that these countries were connected with one another in later Tertiary times. Some of these instances have already been alluded to, such as that of the painted frog, inhabiting Sicily, Malta, and Tunis. It could not owe its existence on the islands to an artificial means of introduction. Major Barrett-Hamilton has shown that the same variety even of a small mammal, the weasel, occurs in Sicily and in Algeria. Among the lizards there is a genus with very short limbs of which a species (*Chalcides ocellatus*) has been met with, not only in Sicily and on the opposite coast of Tunis, but on the islands

of Malta, Lampedusa, and Linosa. These islands form a kind of chain between the southern point of Europe and the coast of Africa.



FIG. 68.—THE PORCUPINE (*Hystrix cristata*), WITH ITS GEOGRAPHICAL DISTRIBUTION IN THE MEDITERRANEAN REGION.

The common wall lizard of Malta belongs, according to Mr. Boulenger, to a distinct variety which is also found in Sicily and Southern Italy.

It is not at all necessary to suppose that an uninterrupted

tableland connected all these countries with one another. It is more likely that a considerable portion of the old land lay to the west of Sicily. Sicily itself may have been partly submerged at the time and partly joined to Malta and Tunis.

The fauna, and the flora too, of North-west Africa really resemble those of Europe so much that, zoologically and botanically, our Continent may be said to extend to the south side of the Mediterranean. The animals and plants of Northern Africa, except Egypt, are, at all events, much more European in character than African.

The peculiarly European operculate mollusc *Pomatias* is quite confined to Europe and North-west Africa, and has been so since Eocene times. Not a single species is known from Egypt, though about a dozen occur in Tunis.

The French zoologist Bourguignat was so impressed by these facts of distribution, that he constructed a map in which North-west Africa is connected by a broad land bridge with Southern Spain, while he assumes that the Atlantic Ocean penetrated to the Eastern Mediterranean right across Africa, between the coasts of Senegal and Tripoli. He thought such geographical conditions prevailed quite recently, at any rate within Pleistocene times. Similar theories have been maintained by other authorities. It has been demonstrated, however, that there are no recent marine deposits in the Sahara. The sea could not, therefore, have invaded that part of Africa in Pleistocene or Pliocene times.

That the sea stretched across the Sahara some time or other within Tertiary times appears probable, for the marine fauna of the Eastern Mediterranean, as first pointed out by Professor Suess, bears a distinct relationship to that of the coast of Senegal. It seems as yet doubtful when that event took place, but the Sahara has for long ages past preserved its character as a formidable barrier in separating the purely Ethiopian from the North-west African fauna.

M. Pallary did not discover a single Ethiopian type of mollusc among the Tertiary fossil land molluscs of Algeria.

The Pliocene deposits of terrestrial molluscs contained but three extinct species, a few forms which have since emigrated, and about 70 per cent. of species still inhabiting the country.

It is surely very remarkable—and I have frequently emphasised the fact in these pages—that the geological age of many of our invertebrates is actually much greater than we have hitherto had any conception of.

It has been proved by M. Pallary's researches that certain forms, such as *Rumina decollata*, have existed in Algeria unaltered since Oligocene times, *Helix pyramidata*, *H. alabastroides*, since the early Pliocene, and many others since the middle of that period.

Rumina decollata (Fig. 69) belongs to the Stenogyridæ, a tropical family of molluscs. It has no near relative in the European fauna. Its general geographical distribution becomes of particular interest since we now learn that it has inhabited Algeria from early Tertiary times. From its North African centre this snail has traversed the Mediterranean on the old land connections north-eastward to Malta, Sicily, Southern Italy, Greece, the islands of Cerigo, Cerigotto, Crete, and to Asia Minor. Northward it crept to Sardinia, Corsica, and Mount Argentaro on the west coast of Italy. The latter formerly belonged to the Tyrrhenian continent. To the north of Corsica it occurs in the caves of Mentone not only fossil, but it still inhabits a broad tract along the coast of the Mediterranean. Possibly it spread from there into Spain, Portugal, Madeira, and the Azores, when the latter were still connected with the mainland of Portugal. From North-west Africa *Rumina decollata* also went westward to the Canary Islands, unless the genus is one of those which originally crossed the Atlantic with a number of other American forms (cf. p. 216), which seems quite possible. In that case the species may be of western origin and may only subsequently have found its way to North Africa.

The mammalian fauna of the North African Tertiary deposits has by no means been exhaustively examined, yet an extremely rich osteological collection has been brought together from

Algeria. It has been shown that several kinds of hippopotamus the rhinoceros, lion, buffalo, horse, wild ass, several antelopes, a camel, and many of the species which had been discovered at



FIG. 69.—*RUMINA DECOLLATA*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

Pikermi, in Greece, had likewise lived in North-west Africa in the past, and had even persisted there to Pleistocene times.

Practically the whole of this rich fauna has vanished from that region, just as our large mammalian fauna has disappeared

from Europe. It has been assumed that the advent of an Arctic temperature killed off these large mammals in Europe. The arrival of northern species in Southern Europe is supposed to indicate a lowering of the temperature all over the Continent, and it has been concluded that the fauna generally was very adversely affected by this change in climate.

But I have pointed out that we can only recognise in Europe an extinction of species on a large scale among the mammals. Here in Algeria a similar extinction of mammalian species has occurred. A few molluscs have died out since Pliocene times, probably fewer than became extinct from any one period to the next following. The Glacial period could not have materially affected the climate of Algeria at any rate, and there is no indication of a change of temperature among the fossils. Nevertheless the larger forms have vanished all the same. Here too we notice, as in Europe, evidences of waves of dispersal which spread over the country. In Europe we have had waves of dispersal of animals from all the points of the compass, and a subsequent extinction as a rule in the direction from which the various species arrived. In the case of North-west Africa many of the large forms remained in the newly conquered territories longer than they did elsewhere, because they were unaffected by any subsequent invasions.

In previous chapters I have several times drawn attention to a group of insects containing many remarkable and noteworthy cases of distribution, namely, the Orthoptera. Our earwigs and grasshoppers belong to this group. Their distribution in North-west Africa has recently been carefully studied by Professor Vosseler, who states that eighty-eight out of the one hundred and eleven species known from that region occur in Sicily as well. This result differs only in so far from that obtained by the molluscs of North-west Africa, as that a considerable number of species are of strictly Ethiopian origin. For locusts and similar insects the desert does not constitute such a formidable barrier as it does for molluscs.

Among the wood lice of North Africa I would particularly refer to one of the species which are in the habit of rolling

themselves into a ball resembling a pill, viz., *Armadillidium quinque-pustulatum*. It is only known from Algeria and Provence, in the south of France. Another wood louse (*Lucasius pallidus*), like our English *Platyarthus*, lives underground in ants' nests. It has not only been discovered in North Africa, but also in Sicily, Sardinia, and the south of France. There are two species of *Platyarthus* too, both living in ants' nests, and both found in North Africa, Sicily, and the south of France. I think these facts of distribution greatly strengthen the view I have already expressed of the former existence of a land connection between North Africa and the south of France by way of Sicily, Corsica, and Sardinia. None of the species mentioned are such as are likely to be conveyed accidentally by plants, and they, moreover, strongly support Dr. Forsyth Major's suggestion of an ancient Tyrrhenian continent.

It might be of advantage now to compare these results with the conclusions deduced from the geographical distribution of plants in the Western Mediterranean area.

Dr. Bonnet informs us that the flora of Tunis does not contain a single plant characteristic of Marocco or Spain, while there are more than a dozen of such from the east. This implies that the east to west dispersal has been much more pronounced than the one in the opposite direction. About 3,000 species of plants are known from Algeria, over 600 of which have a very wide range in Europe. Of the remaining number of plants about two-thirds are indigenous to the Mediterranean region; the rest present special peculiarities of distribution.

To show the affinity existing between the floras of Algeria, Spain, and Sicily, Mr. Mathews states that of the 1,500 species restricted to the western area of the Mediterranean about 1,300 are found in Spain and 900 in Sicily. He concludes that these figures imply the former existence of bridges of land connecting North Africa with Spain and also with Sicily. No less than seventy plants range into Spain westward and reappear in the Eastern Mediterranean, without, however, being known either in Sicily or Southern Italy.

A good many similar cases of discontinuous distribution implying great antiquity have been described.

With regard to the eastern affinity which is so strongly impressed on the Algerian flora, Mr. Mathews comes to much the same conclusion as Professor Engler did. "One explanation, and one alone," he says, "will account for these phenomena of distribution. Sicily, geologically speaking, is of very recent origin; but before its existence the ranges of the Atlas mountains must have extended into Greece."¹ Finally, Mr. Mathews expresses the opinion that this mountain chain extended directly from North Africa to the Lebanon, in Asia Minor, and that Cyprus and Crete are surviving fragments of it.

I have discussed this subject at such length because it seems to me that our European fauna largely owes its complexity of composition to the intricacy and repeated changes of the geographical features in the Western Mediterranean basin. To thoroughly appreciate the fundamental effects of these changes in the disposition of land and water on animal dispersal it became necessary to support my views by zoological and botanical testimony. Before concluding this subject I may quote yet another opinion of one who stands foremost as an authority on the geographical distribution of plants, viz., Professor Engler.

Professor Engler does not specify precisely the geological periods during which the land connections existed, but his studies have enabled him to affirm that plants advanced on land from the Balkan peninsula across Asia Minor, Syria, and North Africa, to Sicily, Southern Italy, Corsica, Sardinia, the south of France, and Spain. It is evident, he remarks, that after Corsica and Sardinia were isolated from their Northern Ligurian connection, and from their Southern African one, which took place early, their flora developed undisturbed, with more pronounced individuality.

Except that Professor Engler makes his plants wander round Syria and North-east Africa to reach Sicily, his views agree with those I arrived at from a zoological study of the problem.

¹ P. 126.

Indeed, he admits that a direct connection between Southern Italy and the Balkan peninsula is quite possible.

I have already treated of the Strait of Gibraltar (p. 98). A few additional notes about its formation, as affecting the fauna and flora in its neighbourhood, will be of interest.

However much difference of opinion may prevail about the former existence of land bridges where now rolls the sea, there is absolute unanimity among zoologists and botanists that the Strait of Gibraltar is due to a recent subsidence of land. The extreme similarity of the fauna and flora to the north and south of the strait is adduced as evidence of this view. Gibraltar, it has often been remarked, is really part of Africa, though we might with equal force claim the whole of North-west Africa as part of Europe.

The point at issue, however, is not so much whether Gibraltar should be considered as part of Africa. The question is rather by what means the North-west African fauna reached Spain and Portugal. That it did so can be proved from many examples. Let us take, for instance, the range of a large and most conspicuous slug belonging to the singular genus *Parmacella*.

Parmacella, as Professor Simroth has indicated, is of Central Asiatic origin. The Mediterranean form (*Parmacella Olivieri*) (Fig. 70), which has received many names, occurs eastward in the Caucasus and on the shores of the Caspian. In the western area it reappears in Algeria, Marocco, and the Canary Islands. On the northern shores of the Mediterranean it is known from a single locality near the mouth of the Rhone, and then again further west from Southern Spain and Southern Portugal.

It evidently is an extremely ancient species, maintaining itself as a relict form in a few isolated spots. It has long since ceased to spread. Closely allied forms, perhaps only varieties, are known from the upper Miocene of the Rhone valley and the Pliocene of Montpellier. It does not appear as if this Eastern French form of *Parmacella* had ever spread into Spain. The *Parmacella* of Southern Spain and Portugal clearly came from Marocco across the Strait of Gibraltar when the latter was dry land.

In Miocene times a broad marine channel, as stated before,

extended between the Atlantic and the Western Mediterranean area across Southern Spain in the region of the Guadalquivir

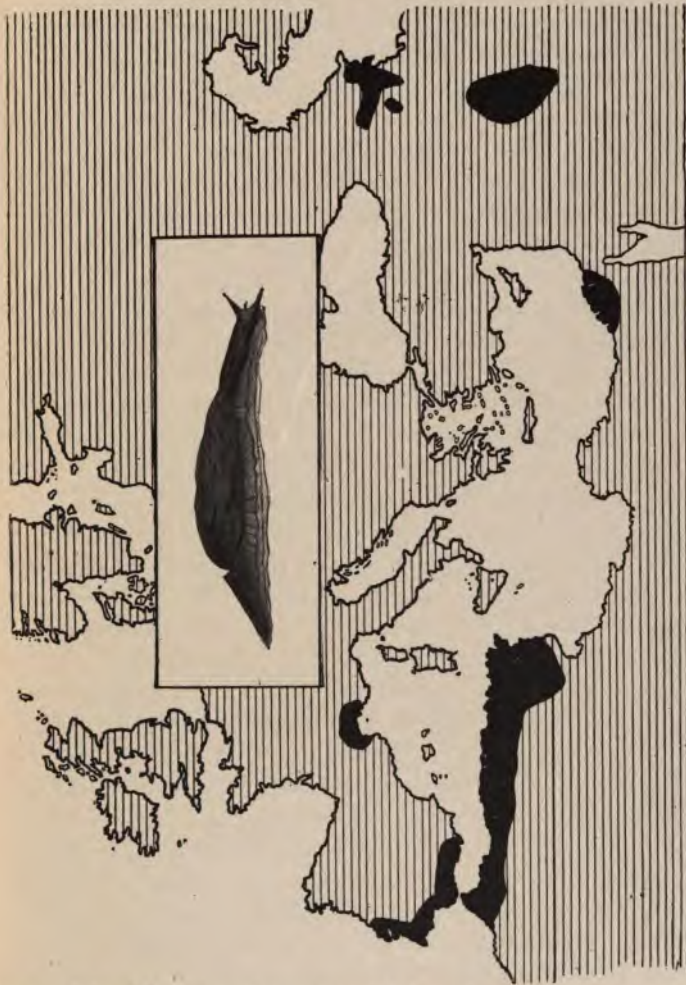


FIG. 70.—*PARMACELLA OLIVIERI*, WITH ITS GEOGRAPHICAL DISTRIBUTION.

river. The Maroccan fauna could therefore advance northward, in Miocene times, across the Strait of Gibraltar on dry land as far as the present site of the city of Granada. Towards the latter

part of the same period the sea invaded Southern Marocco, so that for a time Northern Marocco, together with Southern Spain, became a large island. Parmacella and all the other species which came from Marocco into Southern Spain must have spread northward in middle Miocene times, because at the beginning of the next period, the Pliocene, we find that the sea had gradually invaded Northern Marocco from the south.

Hence the Strait of Gibraltar was formed in early Pliocene times. It has more recently become much narrower, but there is no evidence that Spain and Marocco have been joined since the Miocene period. It was at that time, too, that the marine channel in Southern Spain disappeared, so that the fauna which had accumulated in the southern extremity of that country could spread into Northern Spain and Portugal.

Now we have noticed that the fauna of Madeira and the Azores, which islands were then connected with Portugal, has a certain affinity with that of the Canary Islands. The latter had been joined to Marocco, which received a portion of their fauna. It is thus that some of the Canary Island forms passed through Spain to Madeira and the Azores.

Relict forms are apt to be preserved longer as a rule on islands than on continents. We meet, on that account, with many such on the islands referred to which have vanished from the neighbouring continents.

I do not believe that Madeira and the Azores were connected by land with America. They were only joined to Europe. It is different with the Canary Islands. They must have formed part of the land which connected Africa with America in early Tertiary times.

My opinions are not based on the zoological aspect of the problem alone. Many of our leading geologists, such as Professor Suess, Professor Neumayr, Professor de Lapparent, and others, do not share Dr. Wallace's contention as to the permanence of the great ocean basins. Some of them, on the contrary, hold that a coast-line stretched right across the Atlantic either in early Tertiary or late Secondary times. Among zoologists Dr. Sclater and Professor Osborn adopt this view from a study

of the marine mammalian fauna. Mr. Lydekker, Dr. Blanford, and Dr. von Ihering, have come to similar conclusions, based on their researches on the land fauna.

I have given instances, in an essay on the Atlantis problem, of the geographical distribution of many groups of vertebrates and invertebrates as supporting my views on the Atlantic land bridge. There are two, however, which I have not mentioned, and which have occurred to me since.

It was Mr. Lydekker, I think, who first pointed out that certain rodent mammals, included in the section of the Hystrichomorpha of the South American region, are so nearly akin to those of Africa, that these two continents must have been joined by land to have brought about this remarkable geographical distribution. I quite concur with him. In the countries frequently alluded to in this chapter, in Tunis and Algeria, we find a little stumpy-tailed creature, about the size of a rat, which is able to skip about like a kangaroo with the help of its long hind limbs. It is called *Ctenodactylus gundi* on account of its peculiarly modified inner toes, which are comb-like and are employed for dressing the fur. It has a few near relatives living in South Africa, in Somaliland, and on the west coast of Africa. Extinct forms are known from the Pleistocene of Sicily and from the Pliocene of the south of France. Nowhere in Asia or North America have recent or fossil rodents belonging to this group been discovered. In the West Indies and in South America, on the other hand, they occur from Eocene deposits to the most recent; and numerous species are found still living in the same region. That this group of rodent animals has crossed the Atlantic from South America to Africa in Tertiary times is, therefore, to be looked upon as almost a certainty, and without a direct land connection it could not have done so.

We possess less evidence of a dispersal in the opposite direction from Africa to South America. Yet the frequently cited genus *Clausilia* supplies us with an example.

About seven hundred species of *Clausilia* are known to science, the great majority of which inhabit Europe or did so

formerly. *Clausilias* spread probably from there into Southern or Eastern Asia and Northern Africa. Neither in Northern Asia nor in North America have *Clausilias* ever been discovered; but in South America we once more find them, in Venezuela, Peru, and Ecuador. And it is worthy of note that these South American forms have their nearest relations among the *Clausilias* of the Atlantic islands and Western Europe.

A western branch of the genus no doubt crossed the Atlantic from North Africa to South America in early Tertiary times, and persisted there in small colonies, surrounded by a fauna of a very different type.

The great land bridge across the Atlantic existed evidently in Eocene and Oligocene times. Probably during the Miocene period the northern and southern portions of that ocean became joined. I do not think that early man had made his appearance in Africa or South America at that remote period of geological history. But the fauna and flora of our Continent still bear abundant traces of this union of the New World and the Old, which so profoundly influenced the life of Europe in the beginning of the Tertiary era.

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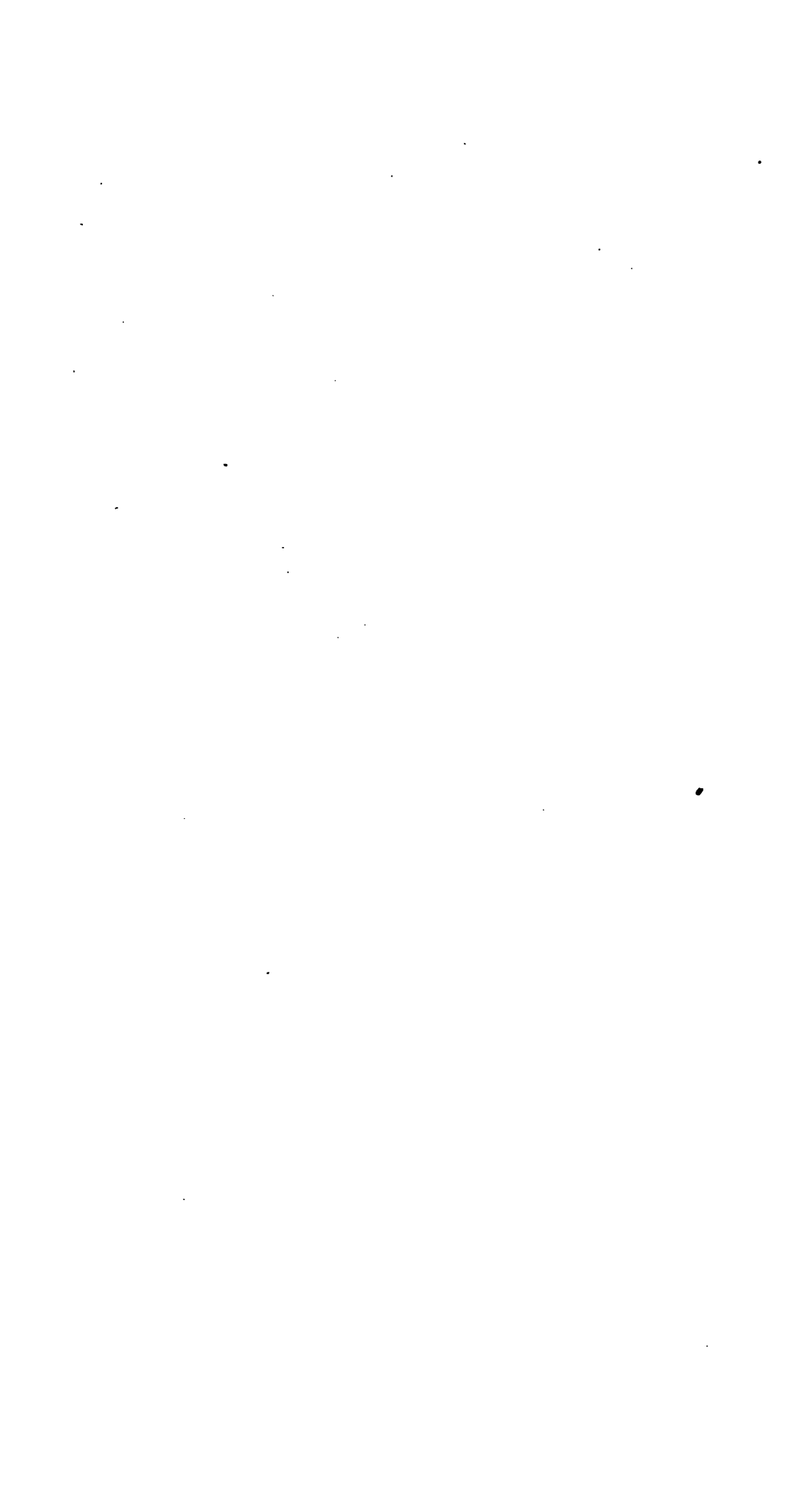
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